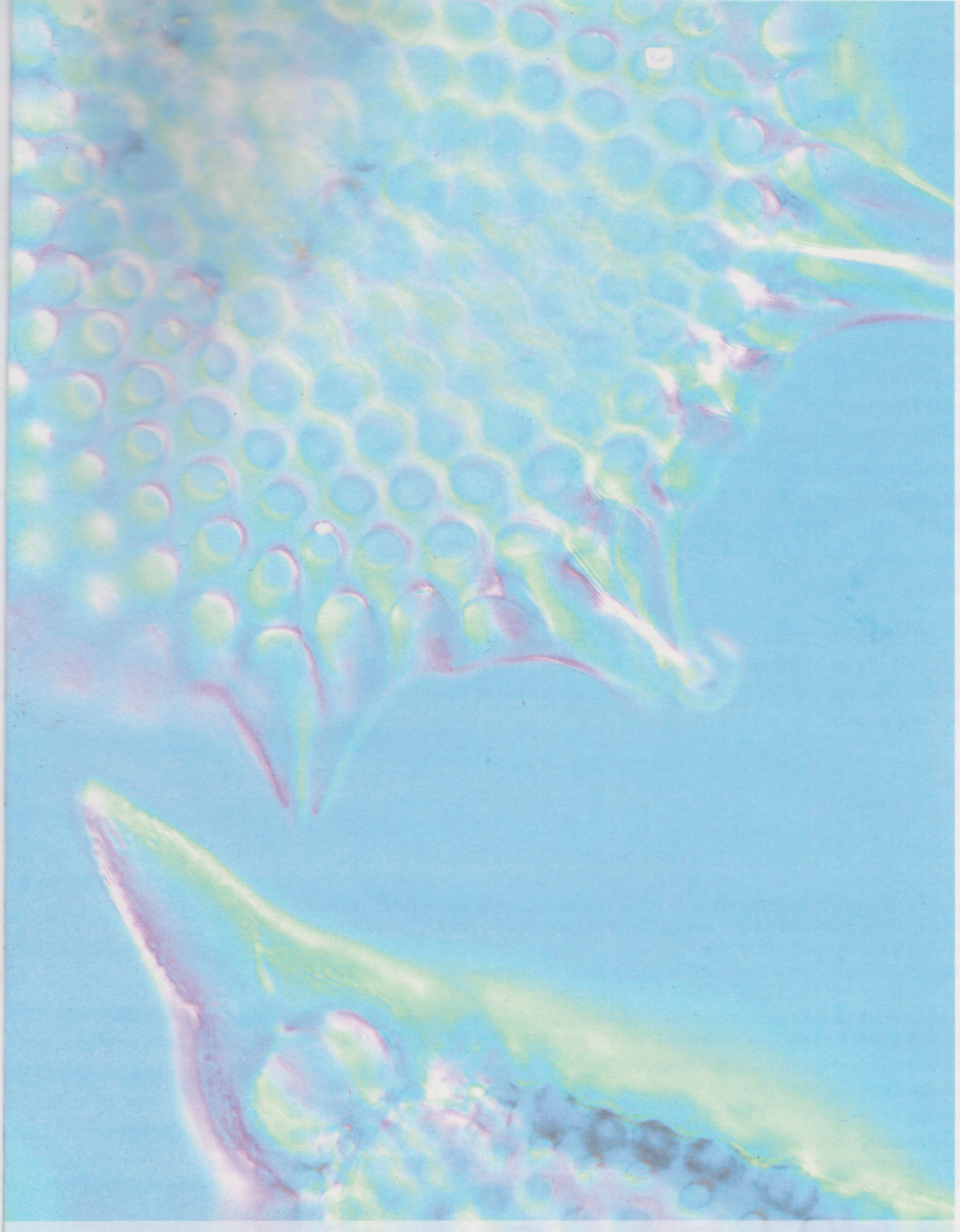
S180

Life in the oceans: exploring our blue planet

Science Short Course

The Open University



Life in the oceans: exploring our blue planet

Angela Colling

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Introduction

This course is based around programmes of the Blue Planet BBC TV series, but whereas that series was very much about animal life in the oceans, this course is about the oceanic environment as a whole, the challenges this environment provides for marine life, and the responses of individual organisms and populations. It is *not* intended to be a comprehensive course in marine biology, and its content is to a large extent determined by that of the Blue Planet programmes.

For the course, the Blue Planet programmes have been put onto three DVDs (some programmes are slightly shortened to take account of overlaps between them). As well as watching complete programmes, you will be able to select particular sequences for closer study.

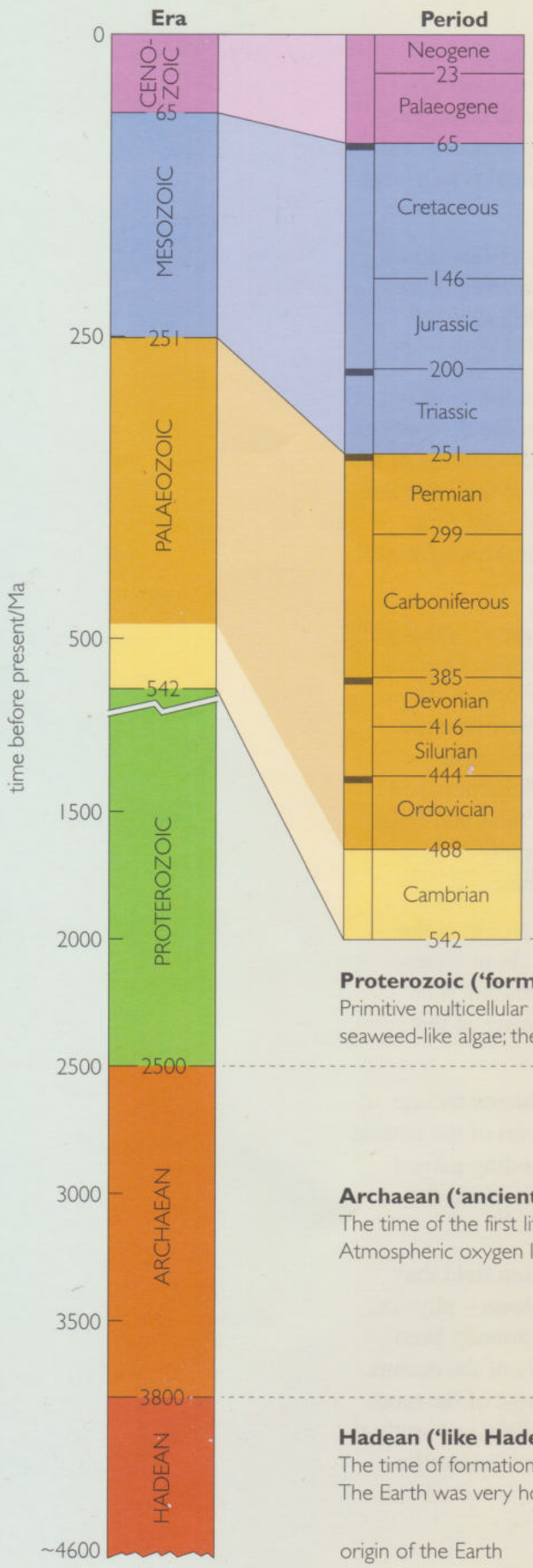
Chapters 1 to 10 of this book are specifically designed to help you get the most out of the Blue Planet programmes. We begin with a brief discussion of how the diversity of life in the oceans has changed over time. This is followed by a brief description of the marine environment itself – the shape of the ocean basins, the nature of seawater and the implications of living in seawater. Chapter 3, on tides and the intertidal zone, should be read with 'Tidal Seas', while Chapter 4 sets up the theoretical background for the enormous biological productivity shown in 'Seasonal Seas'.

Chapter 5 explains why the open ocean is, by contrast, an 'oceanic desert', although certain areas are very rich in nutrients and support abundant life. In 'Open Ocean', you will see powerful hunters like marlin and tuna ranging across the oceans in search of prey, and in Chapter 6 we will look at *how* fish swim, and why tuna are particularly efficient swimmers. Two Open University programmes revise the material in Chapter 6, and also look at why dolphins are such good swimmers and why sperm whales are champion divers. In Chapters 7 and 8 – Coral Seas and Polar Seas – we investigate two contrasting marine environments, again largely concentrating on topics that come up in the accompanying programmes.

Chapter 10, which accompanies 'The Deep', focuses on a particular region of the oceans – the deep sea. The deep sea is largely unexplored, and ideas about it have changed dramatically several times over the last 200 years. For that reason, this chapter adopts an historical approach, at the same time building on many of the scientific concepts introduced earlier in the course.

In Chapter 11, you are asked to consider one of the most serious problems facing humanity at the present time – the global fishing crisis. In this final part of the course, which accompanies 'Deep Trouble', you will be able to use understanding gained earlier to find out more about the causes of overfishing, the results for life in the oceans, and what – if anything – can be done.

Increasingly, scientists are finding that to make progress in their chosen field they need to combine knowledge and understanding from different disciplines – physics, chemistry, biology and geology – i.e. areas of science that have traditionally been isolated from one another. Nowhere is this more true than in the study of the oceans. Bringing together material from a number of different disciplines is one of the most important skills that you will begin to develop during the course. To help you study it effectively, whatever your background, we have provided a Glossary of scientific terms.



Cenozoic ('recent life')
Mammals prospered and diversified, with the earliest hominids appearing ~6 Ma ago

Mesozoic ('middle life')
Dinosaurs appeared, and then mammals, followed by the first flowering plants

This era ended abruptly with mass extinctions of marine animals and dinosaurs, possibly because of environmental disturbances caused by a meteorite impact

Palaeozoic ('ancient life')
Shelled animals appeared, then the first vertebrates (including fish)
Plants moved onto the land, then invertebrates; later, amphibians appeared, then reptiles

The first forests brought about a major increase in atmospheric oxygen levels

During this era, there were major climatic changes (including glaciations); it ended with a mass extinction

Proterozoic ('former life')
Primitive multicellular organisms began to evolve, the earliest of which were simple seaweed-like algae; there were two major glaciations during this time

Archaean ('ancient', 'beginning')
The time of the first life-forms – bacteria, then simple photosynthetic organisms
Atmospheric oxygen levels began to rise during this time

Hadean ('like Hades', 'hellish')
The time of formation of the earliest-known rocks
The Earth was very hot, with extensive volcanism, and there was no life

origin of the Earth

1 What lives in the oceans?

This course is mainly about life in the oceans at the present time, but to understand why there is such a great diversity of marine life, you need to know a little about life in the distant past. To help you appreciate the time-scales involved, begin by studying Figure 1.1, bearing in mind that the times given are in *millions* of years ago.

1.1 Beginnings

We do not know for sure where life began, or when – most scientists think that it began nearly 4000 million years ago in the oceans, or possibly in warm pools on land; others think that life was brought to Earth from space in the form of organic molecules in comets and meteorites. But wherever it began, life first flourished in the sea, and it was here that life-forms first diversified.

There is no direct evidence of the very earliest living organisms, but we do have the remains of early single-celled organisms resembling bacteria. These simple organisms would have used various chemical processes to generate the energy required to build complex biological molecules from compounds in the surrounding environment. By about 2500 million years ago, some of these organisms had developed the ability to photosynthesise – they could use the energy of sunlight to build and maintain their cells (you will learn more about this in Section 1.4).

It was another 1000 million years or so before more complex cells developed. These had well-defined cellular structures, including a nucleus in which the genetic material was held separate from the rest of the cell. This development allowed certain types of cells to come together to form the first simple multicellular organisms: multicellular algae seem to have appeared around 1200 million years ago, and organisms that we would recognise as animals were flourishing by around 600 million years ago. These early multicellular organisms were little more than colonies of single-celled organisms – a similar simplicity of structure can be seen today in sponges, which tells us that they are very primitive animals.

Land plants first appeared around 440 million years ago, though photosynthesising bacteria (see Section 1.3) and fungi may have colonised damp land surfaces by the late Proterozoic (Figure 1.1).

Roughly how long was the gap between the appearance of multicellular algae in the sea, and that of green plants on the land?

If the first multicellular algae appeared around 1200 million years ago, it was another 1200 – 440 = 760 million years before there were green plants on the land.

Figure 1.1 The geological time-scale. Ma = millions of years. Names in capital letters (which you need not remember) are the geological eras, which are major intervals in the Earth's history, determined on the basis of fossils (if present), ages of rock formations (measured using natural radioactivity) and other features of the geological record (e.g. relating to climatic/environmental conditions). For the Palaeozoic onwards, the time-scale is expanded, and is divided into *periods*, which have also been identified as different from one another on the basis of fossils and other features of the geological record. The Neogene and Palaeogene Periods together make up the Tertiary sub-Era. The last 1.8 Ma are known as the Quaternary Period. It will become clear why we have highlighted the Cambrian Period in yellow. Thin black bands indicate the five major mass extinctions of the Palaeozoic and Mesozoic Eras.

Figure 1.2 Modern stromatolites near the Exuma Islands in the Bahamas. Like their ancestors, they are built up of mats of photosynthesising bacteria, which trap sediments and become calcified.

In other words, for 760 million years – about one-fifth of the time that the Earth has existed – there were multicellular organisms in the sea, while the dry land remained essentially barren.

The oldest fossils of recognisable living organisms are of stromatolites, mats of photosynthesising bacteria which built up in shallow marine waters. Stromatolites were very widespread throughout the Archaean (from about 3500 Ma onwards) and for much of the Proterozoic; they began to decline about 850 million years ago, but can still be found in various shallow seas around the world (Figure 1.2).

The fossils we have of the animals living around 600 million years ago are only flattened impressions made in what was once sandy or silty sediment (Figure 1.3). However, they are surprisingly well preserved, perhaps because at that time there were no large predators or scavengers to destroy and scatter remains, and few burrowing animals to churn up the sediment. These early animals seem to have been quite large – some were perhaps a metre across – but they did not have any supporting skeletal hard parts. Most of them were disc-shaped or pancake-like, with a simple sac-like body directly surrounding a digestive cavity reached by a single orifice (i.e. with no separate gut), rather like present-day sea-anemones or jellyfish (Figure 1.3a). Disc-like or tubular organisms are circular in cross-section and so are described as having *radial symmetry*. All later animals have *bilateral symmetry*, with matching left-hand and right-hand sides. As indicated in Figure 1.4, all animal groups that evolved after about 600 million years ago had bilateral symmetry.

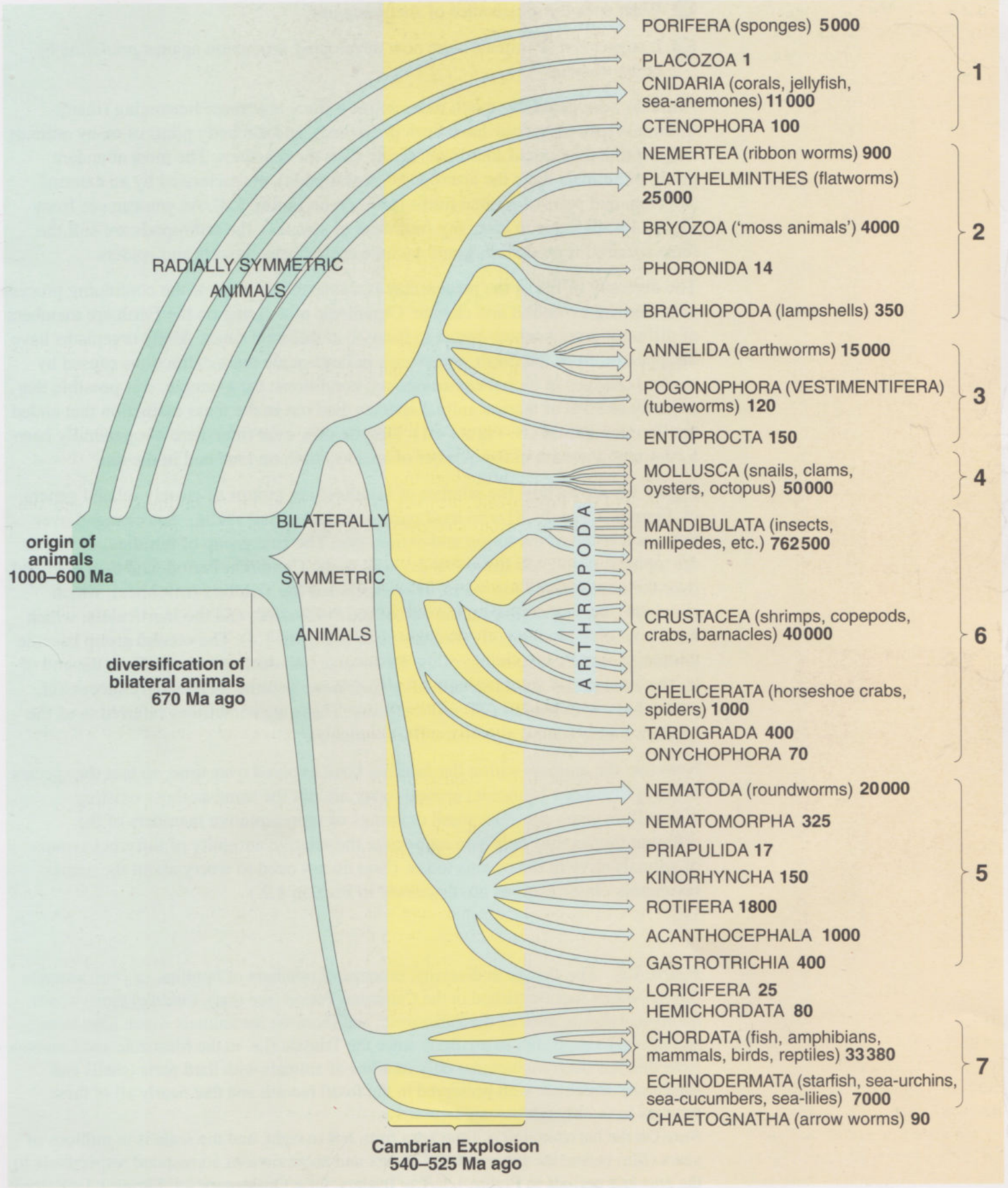
Many radially symmetric animals seem to have gone into decline around 540 million years ago, but around that time there was a great increase in the diversity of other groups of more complex animals. With the 'Cambrian Explosion' of diversity (indicated by the yellow band in Figure 1.4) there appeared animals with identifiable body parts – heads, legs, muscular guts with two openings (mouth and anus) – as well as fluid-filled body cavities. Many animals now had skeletal hard parts, or external shells.

(a)

(b)

Figure 1.3 Fossils of animals which lived around 600 million years ago: (a) *Cyclomedusa*, a jellyfish; (b) *Inkrylovia*, an elongate bag-like animal with transverse partitions. These animals are often referred to as belonging to the Ediacaran fauna, after the Ediacara hills in Australia, where fossils of these and other animals were found in abundance.

Figure 1.4 (*opposite*) Simplified evolutionary tree, showing very schematically how diversification has led to the phyla of animals we know today (listed down the right-hand side in capitals). In this diagram, time goes from left to right (Ma = millions of years). Phyla are the major groups into which organisms are classified on the basis of their body plan. All phyla have marine members, but in this course we will not deal with any animals in group 5. For each phylum, we have given some typical members and (in bold) an estimate of the total number of species (terrestrial + marine) in that phylum.


origin of animals 1000–600 Ma
RADIALLY SYMMETRIC ANIMALS
BILATERALLY SYMMETRIC ANIMALS
diversification of bilateral animals 670 Ma ago
ARTHROPODA
PORIFERA (sponges) 5000
PLACOZOA 1
CNIDARIA (corals, jellyfish, sea-anemones) 11000
CTENOPHORA 100
NEMERTEA (ribbon worms) 900
PLATYHELMINTHES (flatworms) 25000
BRYOZOA ('moss animals') 4000
PHORONIDA 14
BRACHIOPODA (lampshells) 350
ANNELIDA (earthworms) 15000
POGONOPHORA (VESTIMENTIFERA) (tubeworms) 120
ENTOPROCTA 150
MOLLUSCA (snails, clams, oysters, octopus) 50000
MANDIBULATA (insects, millipedes, etc.) 762500
CRUSTACEA (shrimps, copepods, crabs, barnacles) 40000
CHELICERATA (horseshoe crabs, spiders) 1000
TARDIGRADA 400
ONYCHOPHORA 70
NEMATODA (roundworms) 20000
NEMATOMORPHA 325
PRIAPULIDA 17
KINORHYNCHA 150
ROTIFERA 1800
ACANTHOCEPHALA 1000
GASTROTRICHIA 400
LORICIFERA 25
HEMICHORDATA 80
CHORDATA (fish, amphibians, mammals, birds, reptiles) 33380
ECHINODERMATA (starfish, sea-urchins, sea-cucumbers, sea-lilies) 7000
CHAETOGNATHA (arrow worms) 90
1
2
3
4
6
5
7
Cambrian Explosion 540–525 Ma ago

What does the appearance of shells suggest?

It suggests that animals were now developing protection against *predation* by other animals.

Animals were generally much more active – there was more burrowing (many different types of burrow have been preserved), and the body plans of many animals suggest that they could scuttle or 'swim' over the sea-floor. The most abundant group of animals were the arthropods (Arthropoda), characterised by an external skeleton, and pairs of jointed limbs (group 6 on Figure 1.4). As you can see from Figure 1.4, in terms of diversity (numbers of species), the arthropods are still the most successful group today, and include crustaceans, insects and spiders.

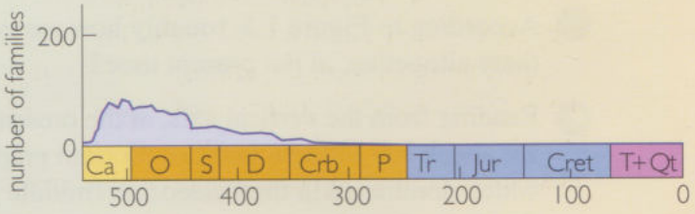
The diversity of life at the present day is a snapshot in time of the continuing process of biological evolution and change. Organisms now living on the Earth are members of different groups which began to flourish at different times. Many organisms have disappeared from the Earth, sometimes in large-scale mass extinctions caused by marked changes in global environmental conditions; for example, it is possible that as many as 95% of marine animal species died out in the mass extinction that ended the Permian Period (cf. Figure 1.1). Despite this, over time there has generally been a continual increase in the number of species, both on land and in the sea.

Figure 1.5 shows how the number of families (i.e. groups of closely related genera, cf. Figures 1.7 and 1.8) with hard parts – skeletons and shells – has changed over time, as a result of evolution and extinctions. The first group of families, shown in the topmost graph, are those that evolved in the Cambrian Period, and then declined over the next 200 million years. These included the Trilobita (trilobites), which eventually became extinct at the end of the Palaeozoic, and the Inarticulata, which were primitive brachiopods (Brachiopoda in Figure 1.4). The second group became dominant near the beginning of the Palaeozoic and declined markedly at the end of it. The final group are those animals which have become increasingly successful, particularly over the last 250 million years. These are sometimes referred to as the Modern Fauna (fauna = animals; flora = plants).

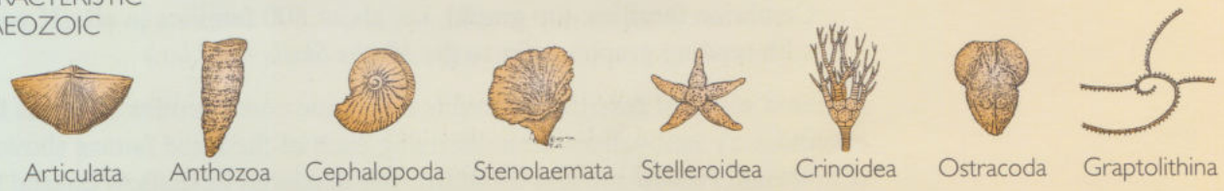
Note that the animals within the families have evolved over time, so that the species of (say) Crinoidea (crinoids) around today are not the same as those existing 400 million years ago. The small drawings of representative members of the different faunas may help you appreciate the relative antiquity of different groups of animals alive in the oceans today. (You do not need to worry about the names; taxonomic classifications are discussed in Section 1.2.)

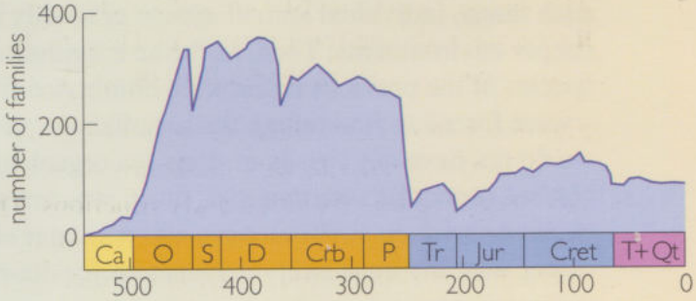
Figure 1.5 The change in diversity, in terms of numbers of families, of (*top*) animals (fauna) which first flourished in the Cambrian Period (see text), (*middle*) those which dominated during most of the Palaeozoic, and (*bottom*) the animals which have been increasingly successful, particularly since the Triassic (i.e. in the Mesozoic and Cenozoic). Note that this diagram includes only families of animals with hard parts (shells and skeletons), which are well preserved in the fossil record, and that nearly all of these families have *only* marine representatives.
Note On the horizontal axis, time goes from left to right, and the scale is in millions of years (Ma) before the present day. Colours and abbreviations correspond respectively to the eras and periods in Figure 1.1; T = Tertiary, Qt = Quaternary (cf. Figure 1.1 caption). Small drawings above the graphs represent some of the classes of animals belonging to the three different faunas. (The terms 'family' and 'class' will be explained in Section 1.2.)

FAUNA CHARACTERISTIC OF THE CAMBRIAN

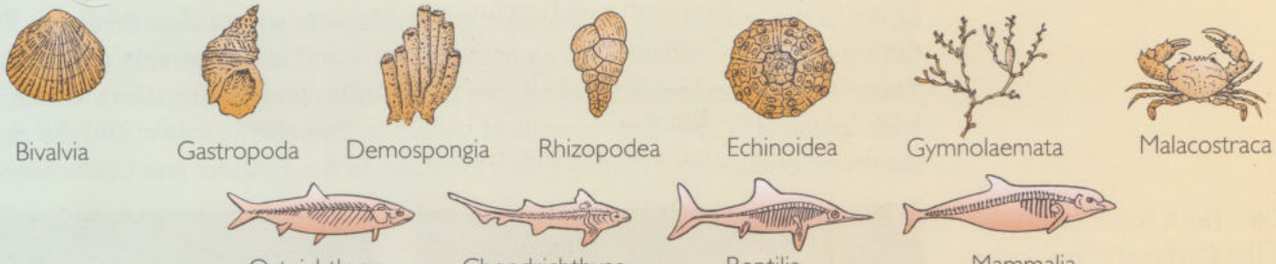


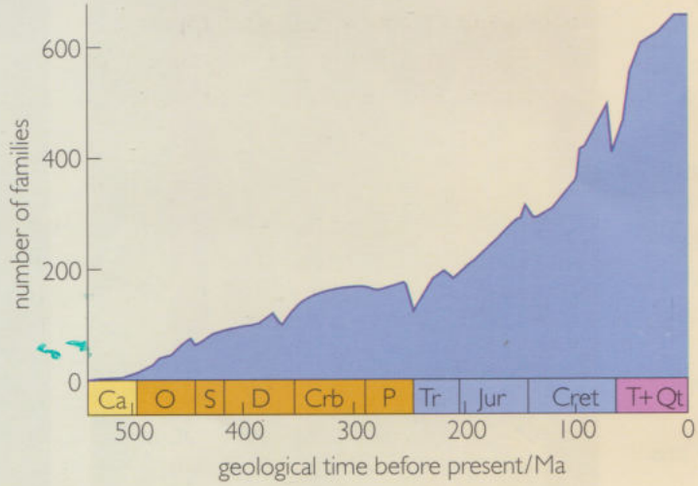
FAUNA CHARACTERISTIC OF THE PALAEOZOIC





'MODERN FAUNA'





Present-day marine animals with hard parts comprise the Modern Fauna (bottom graph in Figure 1.5) plus some of the families which first flourished in the Palaeozoic (middle graph), plus a tiny number of families surviving from the Cambrian (top graph). (Of those animal groups shown in Figure 1.5, only the Trilobita, Hyolitha, Eocrinoidea and Graptolithina are extinct.)

- According to Figure 1.5, roughly how many marine families with hard parts are there altogether, at the present time?

- Reading from the vertical axis, at the present time (0 on the horizontal axis) there are about 700 Modern families (bottom graph) plus about 100 of the families which dominated in the Palaeozoic (middle graph) (plus a negligible number of Cambrian families, top graph), i.e. about 800 families in all. (If you need help with reading graphs, refer to the *Maths Skills Booklet*.)

Detailed study of fossilised remains of marine communities suggests that the evolutionary innovations characterising each of the three faunas shown in Figure 1.5 (Cambrian, Palaeozoic and Modern) first appeared in shallow coastal habitats. Within each fauna, individual animal groups gradually expanded from nearshore habitats to deeper environments. Then, as the next evolutionary fauna moved in, species after species of the previous fauna were eliminated from coastal waters and – it is believed – were forced to find refuge further offshore, generally in deeper water. However, as we do not have any fossils of deep-sea organisms more than about 200 million years old, we cannot be sure that each fauna was not at some time widespread in both shallow and deep environments, and was later eliminated only from shallow waters. Either way, the most likely explanation for disappearances of faunas from shallow environments seems to be predation by newer groups of animals.

Many of the animals of the Palaeozoic Fauna were suspension-feeders – that is, they fed on organic particles floating in the water – and had relatively delicate structures. These included crinoids (also known as sea-lilies and featherstars), which were widespread and abundant in coastal waters in Palaeozoic times, and the somewhat less abundant brittlestars (Figure 1.6). However, in the Jurassic and Cretaceous, fish and

(a)

(b)

Figure 1.6 (a) A fossil brittlestar bed from the Carboniferous Period, more than 300 million years old. From the numerous layers of brittlestars, lying one on top of another, it is thought that this particular area of sea-bed supported a brittlestar community for about 30 years. (b) Part of a large group of unusual crinoids. Their arms (which were 1 m long) are closed together and the 'cups' which carry the arms are somewhat flattened. (*Note* These particular crinoids are from Cretaceous fossil beds, and so are from Mesozoic rather than Palaeozoic times.)

crustaceans living in shallow water evolved to tackle hard-shelled prey, and sea-lilies and brittlestars came under pressure from predators. Today, with the exception of a few locations around the British Isles and northern Europe, large aggregations of brittlestars are rare close to land – indeed, most of the successful suspension-feeders found in coastal waters today have acquired the ability to burrow into soft sediment to avoid predation. However, as you will see in part II of 'The Deep', brittlestars are abundant in the deep sea; similarly, stalked crinoids are today rarely found any shallower than 100 m depth, but are abundant in certain deeper environments.

1.2 Taxonomic classifications

Taxonomy is the science of describing and classifying organisms. In this course, we do not expect you to become taxonomic experts, but during your study you should find that you are becoming clearer about how different marine animals relate to one another.

In Figure 1.4, the names given in capitals down the right-hand side are the various phyla (pronounced 'file-ah') of animals living on the Earth at the present time. A phylum ('file-um') is a group of animals (or other type of organism) whose bodies have a characteristic arrangement, or body plan, which is fundamentally different from those of other groups.

Time goes from left to right in Figure 1.4, and the ways in which the branches come off the main 'trunk' (or off other branches) indicate schematically when a group of animals developed in relation to other groups. For example, a group of phyla which arise from the same point are thought to be the result of a particular period of diversification, in which various forms evolved from a common ancestor. More generally, the phyla in Figure 1.4 are bracketed into groups which are believed to be relatively closely related, i.e. to have had a common ancestor at some time in the past (corresponding to the branching point on the tree). You may be surprised to see that group 7, which includes mammals such as ourselves (in the Phylum Chordata), also includes starfish, etc. (in the Phylum Echinodermata).

The basic unit of classification is the species – animals of the same species are so similar that they could (at least potentially) breed with one another to produce fertile offspring. The bold numbers in Figure 1.4 are the numbers (often approximate) of species in each phylum.

Between the phylum and the species, there are several other levels of classification. Phyla are divided into *classes*, each of which has a different fundamental modification of the basic body plan. The next subdivision down is the *order*, then the *family*, and then the genus (pronounced 'jean-us' or 'jen-us'), which is a group of closely related species; the plural of genus is genera (pronounced 'jen-er-ah'). There are also intermediate subdivisions, such as sub-phylum, sub-order, etc.

Many animals in the ocean have common names, but these vary from place to place and it is not always possible to be sure which animal is being referred to. Every known species of organism has therefore been given a unique scientific name (based on Greek or Latin) which not only identifies it precisely, but also provides information about the group to which it belongs. The first part of the name is its genus, and the second part identifies the species within that genus. For example, the common starfish (i.e. the one which is most common around the British Isles), *Asterias rubens,* is one of six species within the genus *Asterias*. 'Asterias' derives from the Latin for 'star'; 'rubens' refers to the reddish or rosy colour characteristic of

this starfish. The other five species are *Asterias forbesi*, *A. rathbuni*, *A. tanneri*, *A. amurensis* and *A. vulgaris*. Three of these species are named after marine biologists (Forbes, Rathbun and Tanner); 'amurensis' means effectively 'of East Asia' (after the Amur River which flows between China and Siberia, into the Pacific); 'vulgaris' means 'common' – this species is most common off the east coast of North America. You do not need to remember all these details; they are included for interest, and so that you are not put off by other such names when you come across them later. (Note that genera and species names are always italic in printed material. Sometimes, names of genera are used on their own, e.g. *Asterias*; also, if a genus is obvious from the context, we can use its initial letter only, e.g. *A. vulgaris*.)

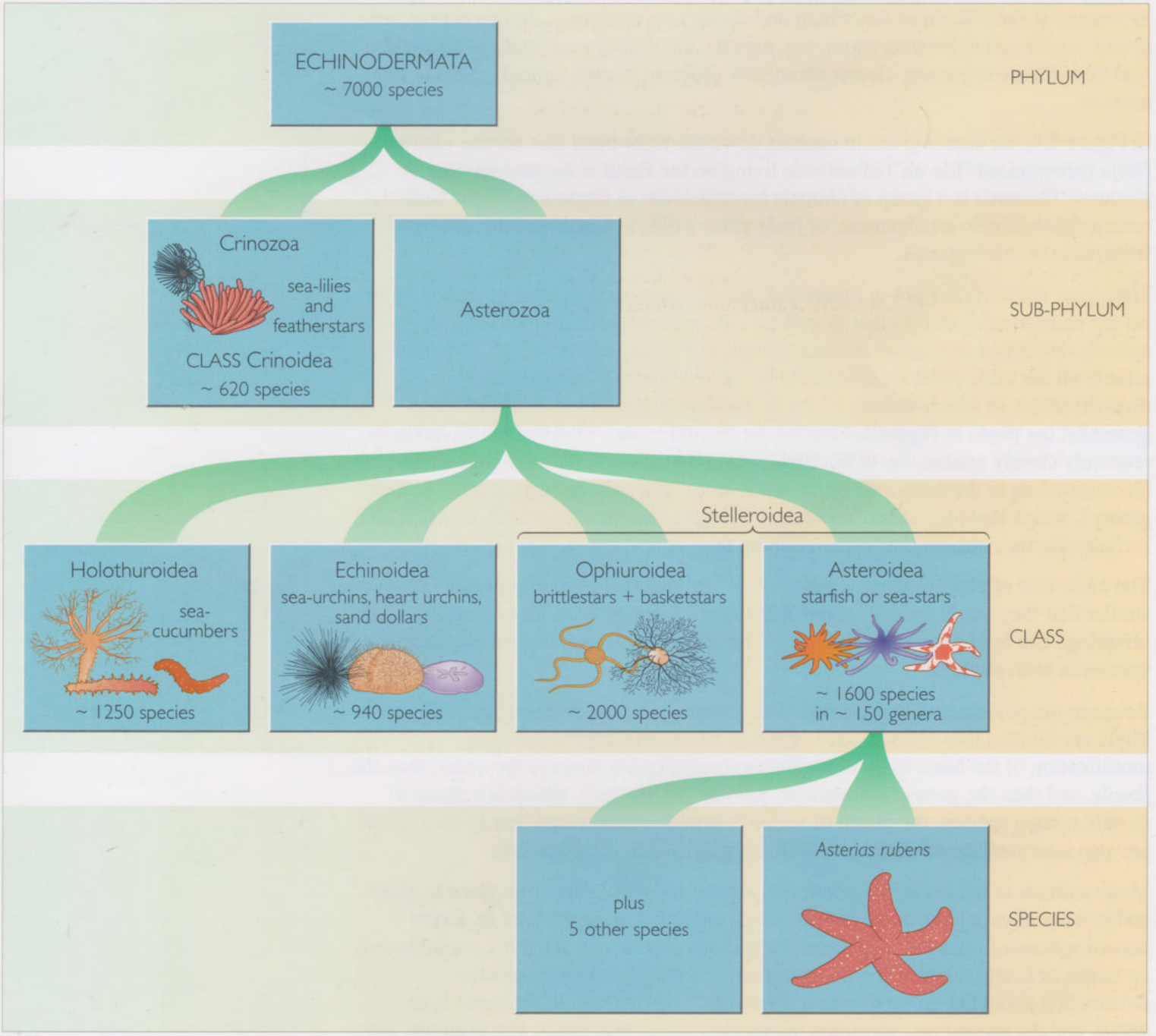


Figure 1.7 Diagram to illustrate how the starfish, *Asterias rubens* (bottom right) fits into the Phylum Echinodermata. (*Note* Fossil echinoderms were much more diverse in form than living ones. Many early forms, now extinct, had very unusual body shapes.)

Asterias rubens and other starfish belong to the Phylum Echinodermata – the echinoderms or 'spiny-skins' (Figure 1.7). Echinoderm skeletons are made up of interlocking calcium carbonate plates and spines beneath an outer skin. All adult echinoderms have the five-point or pentagonal symmetry which is so apparent in starfish (though, as can be seen in Figure 1.10b, their larvae have bilateral symmetry). They all also have a water-vascular system, which you will learn more about in Chapter 7.

There are about 150 genera of living starfish, and they mostly have five arms (or occasionally 15, or some other multiple of five), and they are grouped together into the Class Asteroidea. The Asteroidea make up one class of the Asterozoa ('star animals'); of the other classes, the most closely related to the Asteroidea are the Ophiuroidea, of which there are about 2000 species. The ophiuroids are the brittlestars (mentioned in Section 1.1, see Figure 1.6a) and the basketstars (some of which appear in 'Coral Seas'). Together, the Ophiuroidea and the Asteroidea are known as the Stelleroidea. As shown in Figure 1.7, the other classes are the Echinoidea (sea-urchins etc.), and the Holothuroidea (sea-cucumbers) whose calcium carbonate plates are usually microscopic. There is in fact another class of Asterozoa, not included in Figure 1.7: in 1986, an unusual echinoderm discovered on some wood which had found its way to the deep sea was classified as belonging to the Concentricycloidea ('sea-daisies'). The Asterozoa make up one of two sub-phyla of the Echinodermata, the other being the Crinozoa. The crinoids are the sea-lilies (stalked crinoids) mentioned in Section 1.1 (Figure 1.6b), and the featherstars, which together make up the class Crinoidea. Other classes of crinoids are now extinct.

Figure 1.8 uses the example of two species of whale to demonstrate the classifications used in taxonomy in more detail. Here we have included family, order and sub-order subdivisions, which may clarify the sometimes confusing relationships between different types of whale. (You may find this useful later, when you study Chapter 8.)

One of the tricky aspects of taxonomic classification is that features used to classify animals are sometimes present only at an early stage of the life cycle (e.g. embryo or larval stage). For example, the Phylum Chordata (chordates) includes all animals which at some stage have a skeletal rod (known as a 'notochord'), a hollow nerve cord down the back, and gill slits. Animals of the Phylum Chordata include the Cephalochordata ('head-chords'), the Urochordata ('tail-chords') and the Craniata (craniates, which have brains within skulls), also known as the Vertebrata (vertebrates). This means that vertebrates, including whales and ourselves, are closely related to small and relatively simple marine animals, including sea-squirts and salps (in the case of the Urochordata), and lancelets (in the case of the Cephalochordata). Tunicates have notochords as larvae, and in vertebrates the notochord is present in the embryo but is then replaced by vertebrae (i.e. a backbone). Human foetuses briefly have gills. You do not need to remember these details which are included to explain why taxonomic classifications are not always obvious!

As mentioned above, animals are classified into phyla on the basis of their body plans. Within phyla, however, quite unrelated animals sometimes come to resemble one another because they have similar lifestyles, and evolutionary adaptations have 'solved the problems' associated with this lifestyle in similar ways. This phenomenon is known as convergent evolution.

All known phyla of organisms, living and extinct, originated in the sea, although some later migrated into freshwater or terrestrial environments. In all, there are about 44 marine phyla (opinions vary: a new one was identified in 2001) and 28 terrestrial

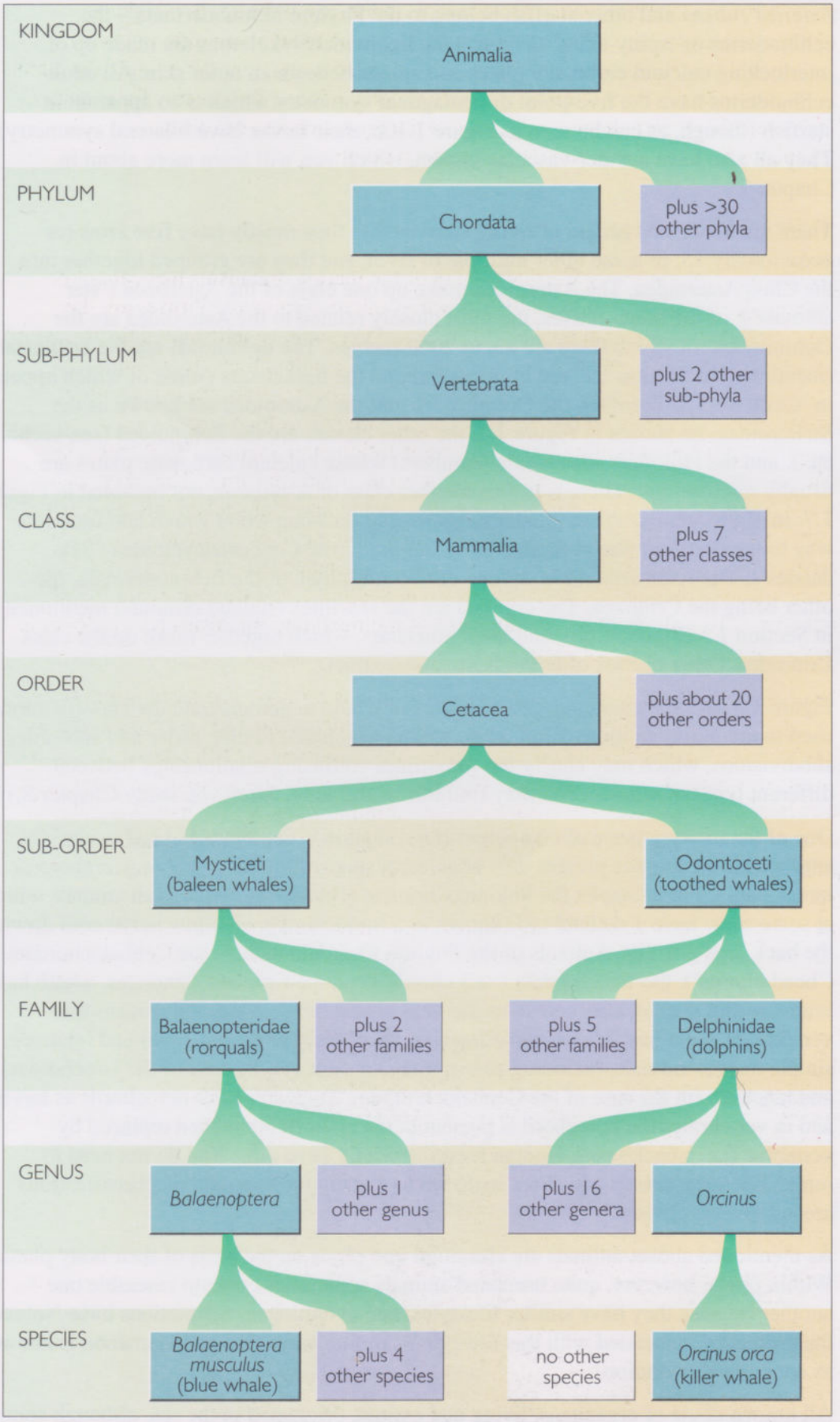


Figure 1.8 Taxonomic hierarchy showing the classification of two related animals that have a high profile in the Blue Planet programmes: the blue whale, *Balaenoptera musculus*, which is a baleen whale (i.e. a plankton-feeder), and the killer whale, *Orcinus orca*, the only species in the genus *Orcinus*.

phyla. Of the 33 animal phyla, 32 have representatives in the sea and 12 have representatives on land. However, there appear to be many more different *species* on land than there are in the sea, perhaps because there is a greater variety of habitats on land. This assessment could reflect a lack of knowledge of the ocean – for example, we have only recently begun to appreciate the great richness of species of small organisms living in the sediments of the deep ocean.

1.3 Micro-organisms

So far, we have not really considered any of the marine organisms that cannot be seen by the naked eye, colloquially known as micro-organisms. Viruses are the simplest living things, but they are little more than some genetic material surrounded by a layer of protein, and cannot grow or reproduce unless they are within another organism, so almost do not qualify as organisms. The most primitive true micro-organisms are bacteria and cyanobacteria (also known as blue–green algae), the latter being the photosynthesising bacteria mentioned in Section 1.1. Present-day bacteria and cyanobacteria are very similar to the first life-forms. They have cell walls (unlike viruses) but do not have their genetic material packed into a nucleus; they are therefore described as *prokaryotes* ('before nucleus'). Organisms which have cells with nuclei are known as *eukaryotes* (pronounced 'you-carry-oats' – the name means 'true nucleus'). As alluded to in Section 1.1, it was the evolution of eukaryotes that allowed the development of multicellular organisms (corresponding to the far left-hand side of Figure 1.4).

Single-celled organisms (with nuclei) are known as protists. The term covers a range of different types of organism, including single-celled algae (e.g. coccolithophores; Figure 1.9), single-celled animals (or protozoans, *zoon* = animal), and single-celled organisms that have characteristics of both plants and animals. Notable amongst single-celled animals in the oceans are the foraminiferans (which have intricate chambered shells made of calcium carbonate) and the radiolarians, which have delicate external skeletons of silica, often with spines (Figure 1.10a, overleaf). All species of radiolarians and many foraminiferans drift in the upper ocean, and so are described as *planktonic* (drifting); in particular they are known as *zooplankton* (i.e. animal plankton). Figure 1.10b shows a group of multicellular zooplankton (amongst which are the larvae of various marine invertebrates), along with some copepods

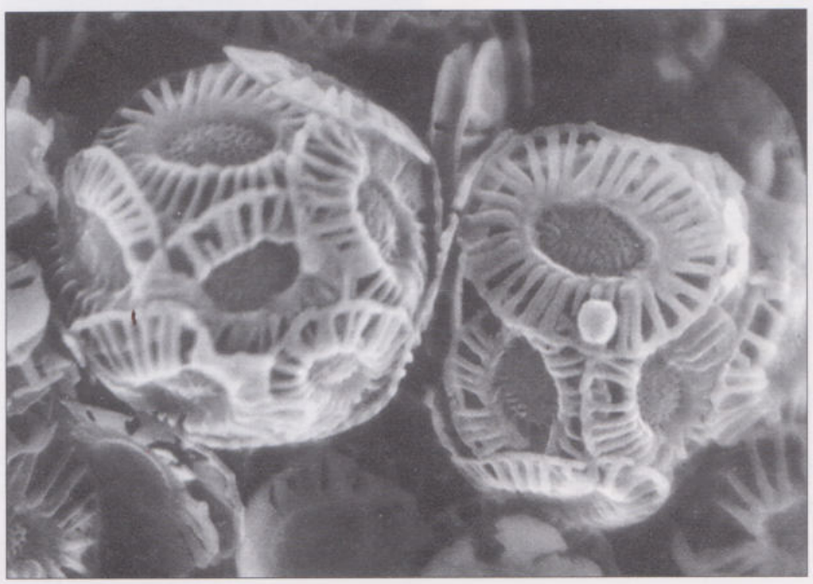
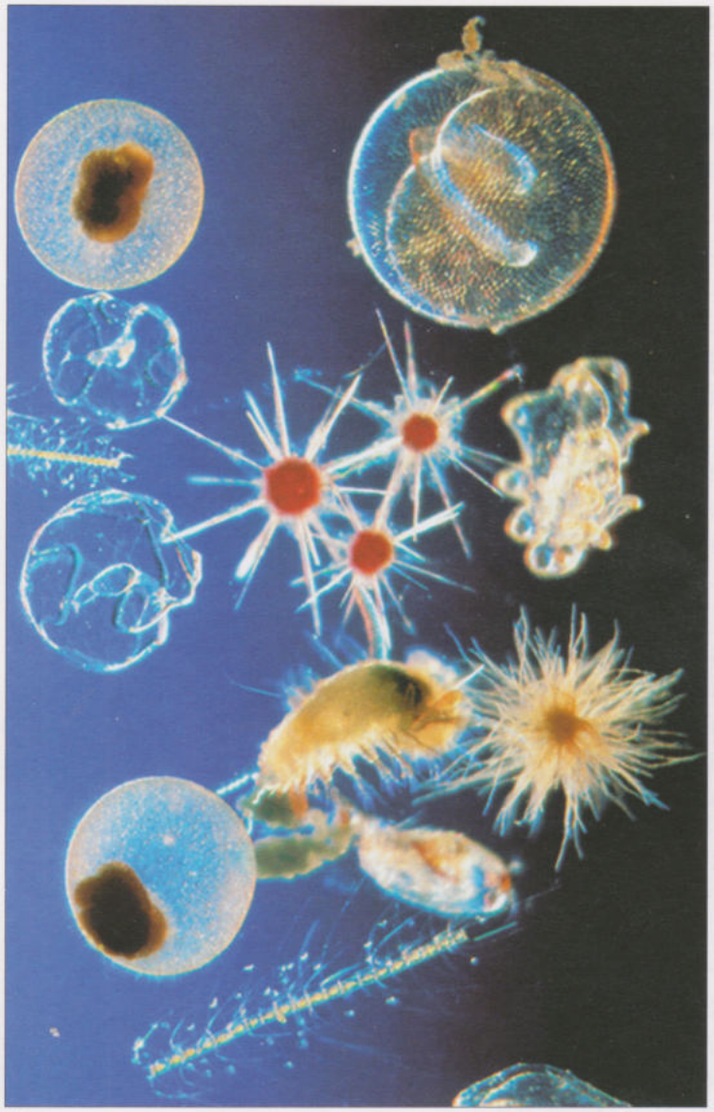
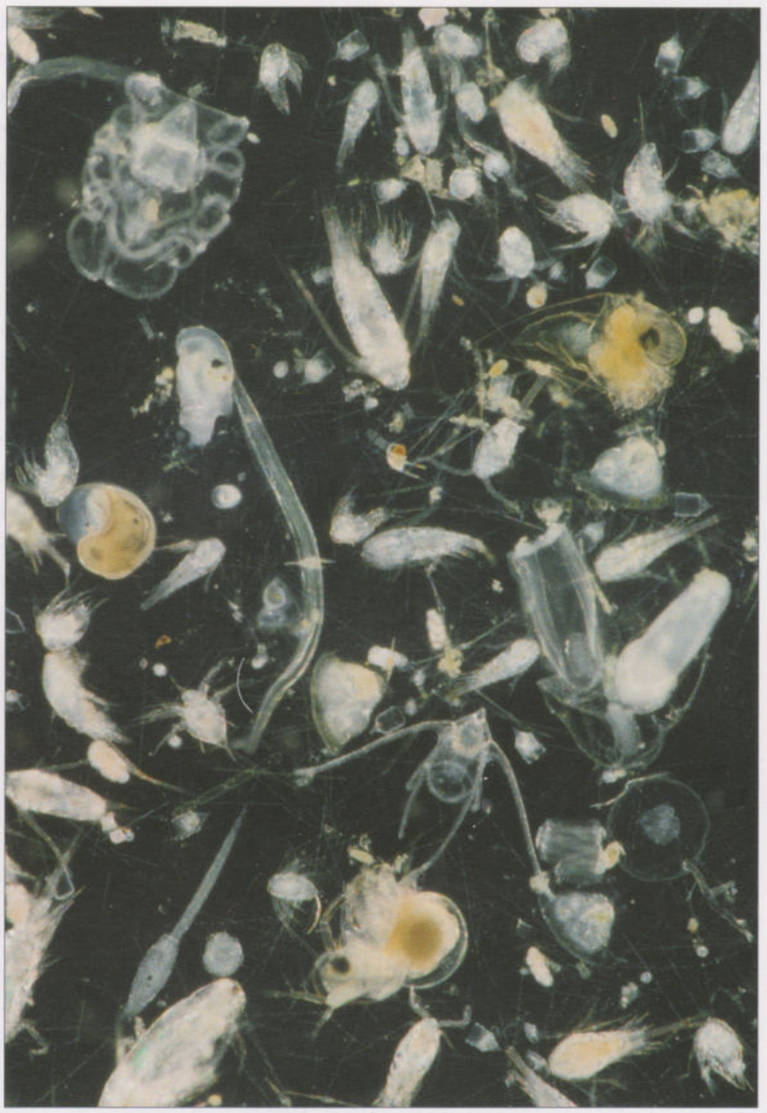


Figure 1.9 Two specimens of the coccolithophore *Emiliania huxleyi*, the most abundant species of coccolithophore in the world's oceans; the small particle on the right-hand coccolithophore is a virus. Coccolithophores get their name from the platelets of calcium carbonate ('coccoliths') which surround the algal cell. These two coccolithophores are lying amongst loose coccoliths which have been shed during virus infection. The coccolithophores are about five-thousandths of a millimetre (5 microns or 5×10^{-6} m) across. (If you have not come across such small numbers before, refer to the *Maths Skills Booklet*.)



(a)



(b)

(c)

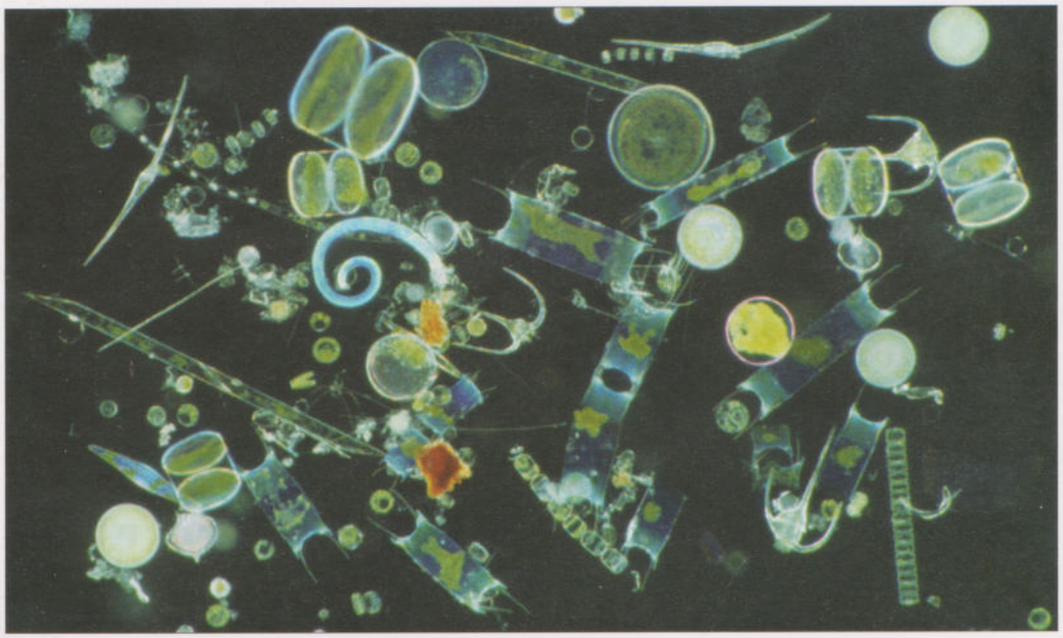
Figure 1.10 (a) A group of planktonic organisms, mainly zooplankton. In the centre of the image is a group of spiny radiolarians. Below these is a crustacean larva, and, below that, a female copepod (planktonic crustacean) with two egg sacs (partly concealed). The two round objects on the left-hand side are fish eggs. There are two 'hairy' chains of diatoms (phytoplankton), one on the far left and one at the bottom; the one at the bottom is a few tenths of a millimetre long.
(b) A group of zooplankton, including small copepods and copepod larvae. Several are the planktonic larvae of various marine invertebrates, some of which are bottom-living species. The two animals with brownish coloration, at the bottom and on the far left, are larval molluscs. There are two larval echinoderms: the animal at top left is probably a larval starfish, while the creature with the long curved spines, just above the molluscs at the bottom, is a brittlestar or sea-cucumber. The jelly-like 'tube' is a salp. On the left-hand side, just below the larval starfish, is an animal with a long curved tail which looks separate from the body; this is an appendicularian, or 'larvacean' (closely related to sea-squirts); the small 'tadpole' below is probably another. The field of view is about 1.25 cm across.
(c) A group of copepods of the species *Calanus finmarchicus*, each about 2 mm long. Copepods are probably the most abundant group of zooplankton in the ocean.

(planktonic crustaceans); one of the most common species of copepod in the northern North Atlantic and the waters around the British Isles is *Calanus finmarchichus*, shown in Figure 1.10c. Zooplankton may be herbivores, feeding on phytoplankton, carnivores feeding on other zooplankton, or they may be detritivores, feeding on organic material. Many are omnivores, with a mixed diet of plant and animal material.

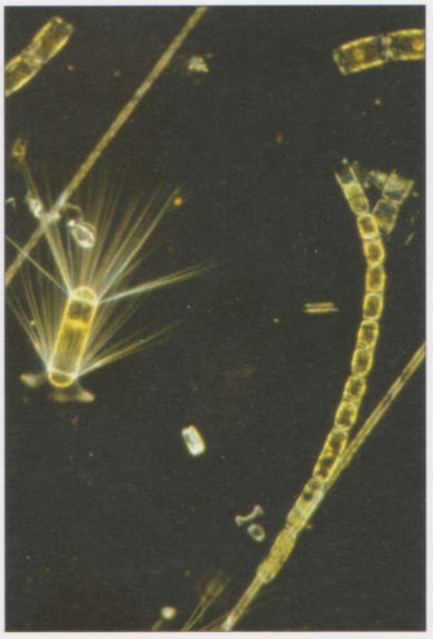
Taxonomists now distinguish aquatic algae (some of which are very simple organisms) from plants (which produce seeds, and have roots). In this course, for simplicity, both land plants and algae will be referred to as plants. The great majority of marine algae are single-celled floating organisms, collectively known as *phytoplankton* (*phyton* = plant) or planktonic algae (Figure 1.11). In high-latitude and temperate seas, the most conspicuous phytoplankton are often species of diatoms, which have external skeletons made of silica; some species of diatom have spines, some have a pill-box shape or are elongate (Figure 1.11a), and others form chains (Figure 1.11, particularly part b). You may spot some or all of these types of diatom in the Blue Planet programmes (note that, like all phytoplankton, they are very small, ranging from two-thousandths of a millimetre to one millimetre across). After diatoms, the second most conspicuous phytoplankton are often the dinoflagellates, some species of which feed on small zooplankton and other phytoplankton, and so resemble animals more than plants. In terms of numbers of individuals, the most abundant phytoplankton are usually extremely small species, collectively known as 'picoplankton'.

The term algae (singular: alga) was originally used to mean any simple plant-like organism (found in the sea, in ponds, or on damp tree trunks, paths and walls). As far as marine life is concerned, the term algae is now used to include not only phytoplankton and some simple bottom-living algae, but also seaweeds – sometimes referred to as macro-algae (i.e. 'big algae'). Like phytoplankton, seaweeds are surrounded by their 'growing medium' – water plus nutrients. Because they take in nutrients from the surrounding water, seaweeds do not need a system to transport water up into the plant. They also do not need roots as such, although they do have structures known as *holdfasts* so that they can remain fixed in one place. Furthermore, as they are supported by the surrounding water (and sometimes also by gas bladders), they do not need the strengthening woody structures found in land plants.

Figure 1.11 (a) A collection of phytoplankton, mainly diatoms and dinoflagellates. The diatoms include elongate and round ('pill-box'-shaped) species, and some chain diatoms. The small pale-coloured algae are dinoflagellates, as are the distinctive ones with three spines, which belong to the genus *Ceratium*. Field of view about 1.25 mm across. (b) Various species of chain diatom, collected in the Southern Ocean (the ocean which surrounds Antarctica).



(a)



(b)

1.4 Plants and bacteria: making organic material and breaking it down

Plants have been largely responsible for the evolution of our atmosphere. Before plants (algae, initially) became abundant, concentrations of oxygen in the atmosphere were very low, which in turn had implications for the types of animals that could evolve. With increasingly abundant plant life, more and more oxygen was released into the atmosphere.

This 'new' oxygen was produced as a by-product of photosynthesis, the process whereby plants build their own organic material by harnessing the energy of sunlight to combine atmospheric carbon dioxide (CO_2) with water (H_2O) to produce a range of carbohydrate compounds (e.g. starches, sugars, cellulose). Expressed in words, the process of photosynthesis can be written as follows:

$$\underset{\text{(from the atmosphere)}}{\text{carbon dioxide}} + \text{water} + \text{light energy} \rightarrow \text{carbohydrate} + \text{oxygen} \qquad (1.1a)$$

Animals cannot build their own organic material and so have to rely on plants, either directly (if they are herbivores) or indirectly (if they are carnivores). In order for plants and animals to make use of organic material such as carbohydrate, it has to be broken down (metabolised) into all the different substances an organism requires in order to live. The energy needed for all these processes is released from carbohydrate (and other organic molecules) by a process known as respiration. Respiration can be expressed in a 'word equation' as follows:

$$\text{carbohydrate} + \text{oxygen} \rightarrow \text{energy} + \text{carbon dioxide} + \text{water} \qquad (1.1b)$$

Do you notice anything interesting about this equation?

The equation for respiration (1.1b) is the *reverse* of the equation for photosynthesis (1.1a). Note also that while photosynthesis captures or *fixes* energy, respiration releases it.

All living organisms need to respire. In the case of air-breathing marine animals (mammals and reptiles), oxygen is taken in with air into the lungs, and carbon dioxide is breathed out. In the case of planktonic organisms and most marine animals, the oxygen for respiration is taken up from oxygen dissolved in seawater, and the waste carbon dioxide is returned to solution in seawater. During photosynthesis, phytoplankton take up carbon dioxide from solution in seawater and release oxygen into solution in seawater.

Eventually, all organisms die. In the oceans, as on land, dead organic material is broken down by bacteria. In environments where oxygen is present, bacteria break down dead tissue in a process resembling respiration (cf. Equation 1.1b), and so release the components of the organism back into the seawater. These components are not only the elements present in carbohydrates (carbon, hydrogen and oxygen) but also other constituents essential for life, which are sometimes in short supply. We will come back to this topic in Chapter 4.

In this course, we will be concentrating mainly on animals. However, it's important not to forget the fundamental role of plants in making organic material that is then available to support other organisms, and of bacteria in breaking it down so that its 'raw materials' can be re-used.

To consolidate what you have learnt in this chapter, we recommend that you now use what you have just read to answer the following questions.

Question 1.1

(a) According to Figure 1.4, to what phylum do corals belong?

(b) To which of the following three types of animals are corals least closely related: sponges, jellyfish, sea-anemones? ◀

Question 1.2

Which representatives of the Phylum Echinodermata, (1) characteristic of the Palaeozic, and (2) part of the Modern Fauna, are illustrated in Figure 1.5? ◀

Question 1.3

Would you say that the five major mass extinctions of the Palaeozoic and Mesozoic, indicated in Figure 1.1, can also be seen in the graphs in Figure 1.5? ◀

2 Introduction to the marine environment

This chapter does not relate specifically to any particular Blue Planet programme, but in a sense it 'sets the scene' for all of them. Here we introduce terms, topics and concepts that will be useful in later chapters.

It is frequently said that 'the oceans cover about 70 per cent of the planet', but this phrase does not really convey very much about the size and nature of the 'living space' available to marine organisms. For one thing, organisms may live on the sea-bed, or in the body of the ocean (sometimes referred to as 'the water column'). The first group of organisms are described as *benthic* or the 'benthos' (Greek for 'depth'), and the second group are described as *pelagic* (after *pelagos*, Greek for 'ocean'). Planktonic organisms (or, as a group, 'plankton') are those that live in the water column and cannot make their way against a current; pelagic animals capable of swimming against a current (e.g. fish, adult squid) are described as *nektonic* (or, as a group, 'nekton'). Living conditions for both benthic and pelagic organisms are greatly affected by where they live in relation to the sunlit surface layers. Of course, the most distinctive aspect of living in and around the oceans is that it involves being continually (or, in the case of some organisms, periodically) submerged in salty water.

2.1 What is seawater?

The oceans contain 97 per cent (%) of the water on Earth. Most of the rest is locked up in ice-caps and glaciers, and the remainder is in lakes, rivers, streams and groundwater (in rocks and soil), and in the atmosphere as water vapour and clouds. While the water in the ice-caps and glaciers may remain there for thousands of years, rivers continually flow into the sea, and water is continually evaporating from the surface of lakes and the ocean (particularly at low latitudes), forming clouds, and releasing precipitation (rain, snow, hail) over land and sea. Groundwater, too, is continually seeping into the sea, while being recharged by rainwater from above. This continual cycling of water through different natural 'reservoirs' is known as the hydrological cycle (or 'water cycle').

Rivers flowing into the sea carry with them not only solid particles of mud, silt and organic material, but also substances that have been leached from the minerals in rocks by rainwater – these are in *dissolved* form, i.e. they are no longer solid (you couldn't get them back, even with the finest sieve) and their constituents are separated from one another by large numbers of water molecules. Here is a simple analogy: imagine that you took a chunk of rock salt, put it in a bowl and continued to pour water over it until it had apparently vanished – it would no longer exist in its solid form, but its constituents would now be *in solution* in the water in the bowl. Rock salt is made up of crystals of sodium chloride, which has the chemical formula NaCl (Na for sodium, Cl for chlorine); sodium chloride crystals are made up of *ions* of sodium, written Na^+ (these are sodium atoms that have each lost an electron, and so have become positively charged) and chloride ions, written Cl^- (chlorine atoms that have each gained an electron, are so are negatively charged). In solid rock salt, the ions are bound together, and the positive and negative charges cancel out. When rock salt dissolves, water molecules, which are themselves weakly charged, effectively pull the ions apart and come between them, so that the ions become

independent from one another. If you warmed your solution of sodium and chloride ions (or left it to stand for some time), the water would gradually evaporate away, and eventually solid rock salt would recrystallise.

Dissolved constituents such as sodium and chloride are sometimes referred to as 'dissolved salts', even though they are separate ions and not salts at all. Greater or lesser amounts of all the 92 naturally occurring elements have been measured or detected in seawater, but sodium and chloride, plus nine others, are by far the most abundant, together making up 99.9% of the dissolved constituents in seawater (Table 2.1).

Rivers have been flowing into the sea for billions of years, and you would be forgiven for thinking that the oceans must therefore be continually getting saltier and saltier. However, this is not the case, because an equilibrium situation has been reached, whereby the rate at which each constituent is being removed (e.g. by chemical reactions with sea-floor rocks) is balanced by the rate at which it is being supplied in rivers. The concentration of dissolved constituents in seawater – its *salinity* – is, on average, about 35 grams of dissolved ions ('salt') in every litre of seawater. By convention, this is often simply written as 35, with no units.

Because seawater contains dissolved constituents, its density is greater than that of freshwater: a cubic metre of seawater weighs about 1030 kilograms (kg), while a cubic metre (1000 litres) of freshwater weighs almost exactly 1000 kg.

How does this affect the buoyancy of organisms in seawater?

As you will know if you have swum in both freshwater and seawater, it is much easier to float in seawater, i.e. seawater provides greater buoyancy than freshwater.

Buoyancy in marine organisms will be discussed in Chapter 6.

Seawater also contains dissolved gases; these are by and large the same gases that are found in the atmosphere. As in the atmosphere, the most abundant gases in seawater are nitrogen (N_2), oxygen (O_2), argon (Ar) and carbon dioxide (CO_2). However, their relative proportions in seawater differ from those in the atmosphere because they dissolve in seawater to different extents, and (with the exception of argon, which is inert) their distribution within the ocean is affected by their participation in biological and chemical reactions.

Can you suggest which gas is actually *added* to surface waters as a result of biological activity?

Oxygen. As you read in Section 1.4, photosynthesis by marine plants produces this gas as a by-product.

As a result of photosynthesis, and the fact that oxygen is forced into solution in seawater when air bubbles formed at the crests of waves are churned down into the water column, surface waters are generally supersaturated with oxygen, i.e. contain more dissolved oxygen than would normally be dissolved in seawater at that temperature. However, as oxygen is used by *all* organisms in respiration, and particularly by bacteria in decomposition of dead material, its concentration generally declines in the top 500–1000 metres (m) of the ocean.

The atmospheric gas that dissolves most readily in seawater is carbon dioxide – it is in fact a special case, because dissolved CO_2 reacts with water and so exists in seawater in a number of different forms. So while nitrogen is the most abundant gas

Table 2.1 The 11 most abundant ions in seawater, in order of decreasing abundance. Where it is not obvious, the atoms from which they form are given in brackets. As electrons are negatively charged, an atom that *gains* an electron becomes a negatively charged ion, and an atom that *loses* an electron becomes a positively charged ion. In the case of ions of magnesium, calcium and strontium, each atom has lost two electrons; in the case of sulfate, two electrons have been gained. (*Note* You do *not* need to remember this list.)

Name	Ion
chloride (chlorine)	Cl^-
sodium	Na^+
sulfate (sulfur, oxygen)	SO_4^{2-}
magnesium	Mg^{2+}
calcium	Ca^{2+}
potassium	K^+
hydrogen carbonate 'bicarbonate' (hydrogen, carbon, oxygen)	HCO_3^-
bromide (bromine)	Br^-
borate (hydrogen, boron, oxygen)	$H_2BO_3^-$
strontium	Sr^{2+}
fluoride (fluorine)	Fl^-

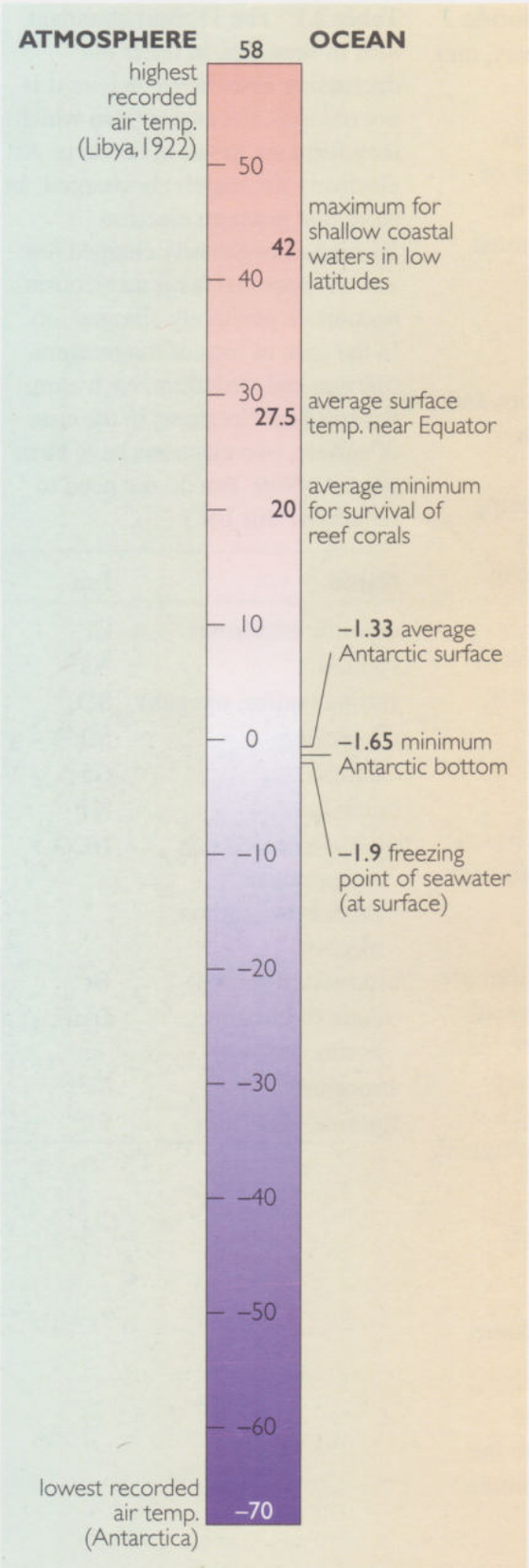


Figure 2.1 Characteristic temperatures in the sea (right) and on land (left). Temperatures are given in degrees Celsius (°C). *Note* If you are not sure how to use minus numbers, refer to the *Maths Skills Booklet*.

in the atmosphere, carbon dioxide is the most abundant gas in the ocean. For all gases, the colder the seawater is, the more dissolved gas it can hold.

Seawater contains a huge range of particles in suspension, some living (viruses, bacteria and phytoplankton), some of organic origin (faecal pellets, debris from dead organisms), and some inorganic (e.g. clay brought down by rivers, dust carried out to sea on the wind).

Last but not least, there are organic substances dissolved in seawater – by-products of the metabolism of living organisms and the decomposition of dead organisms.

2.1.1 Seawater: a most unusual liquid

Water is an unusual liquid in many ways, and seawater is stranger still. It is not possible to go into all its properties here, but we should look briefly at some of the most important, from the point of view of life on Earth.

Water has a very high specific heat – that is, it takes more heat energy to raise the temperature of a given volume of water by 1 °C than it takes to raise the temperature of any other liquid (with the exception of liquid ammonia) by the same amount. An important consequence of this is that the ocean heats up more slowly than the continents in the summer, and cools down more slowly than the continents in the winter. As a result, temperatures in the ocean fluctuate within a much smaller range than those in most terrestrial habitats (see Figure 2.1).

- If the maximum sea-surface temperature in the tropics is about 30 °C, how many times greater is the temperature range on land compared with that in the seas and oceans, according to Figure 2.1?

- Throughout the ocean as a whole, temperature ranges from –1.9 °C (the freezing temperature of seawater) in some polar regions, up to about 30 °C, i.e. a range of about 32 °C (or about 44 °C if we include shallow tropical waters). The temperature range on land (between the two extremes given) is from about –70 °C up to about +58 °C = 128 °C. The temperature range on land is therefore 3–4 times greater than that in the seas and oceans (depending on which values we use).

The latent heat of vaporisation of water is probably the highest of *all* substances. In other words, more heat energy is needed to convert a given mass of liquid water to a gas (i.e. to water vapour) than would be needed to convert the same mass of any other liquid to its gaseous form. This means that enormous amounts of heat are taken up from the surface of the ocean when water is converted into water vapour (i.e. evaporates) and is carried away by the atmosphere, to be released when the water vapour condenses to form cloud in a cooler environment. This, along with the high specific heat of water, means that the oceans play a huge role both in controlling the global climate and in influencing climate locally (the role of the Gulf Stream in transporting heat from lower latitudes towards north-western Europe is well-known).

Another unusual property of water relates to the way in which its density changes with heating and cooling. Most liquids simply expand and become less dense when they get warmer, and contract and become more dense when they get colder, becoming denser with continued cooling even

after they have become sufficiently cold to solidify (i.e. to freeze). Water, on the other hand, becomes least dense when it is coldest – ice floats on water. Imagine how different the world would be if ice sank! As suggested above, seawater (unlike freshwater) cools all the way down to –1.9 °C before freezing. As you will see in Chapter 10, this has important consequences for life in the deep ocean.

What other properties of water can you think of?

A property of water that may immediately have come to mind is that it is transparent; more specifically, it is transparent to visible light, with the result that you can see through it. However, water is not *completely* transparent to visible light – if it were, you would be able to see the sea-floor from a boat even in very deep water, and the deep ocean would be as well illuminated as the land! Furthermore, it is much less transparent to thermal (infrared) radiation, and hardly transparent at all to ultraviolet radiation. We will have a closer look at these topics in Chapter 4.

In contrast to radiation, sound is transmitted through the ocean with relatively little absorption. Sound travels through air or water, or any other medium, as a wave in which compressions of the air/water (molecules coming closer together) alternate with rarefactions (molecules moving further apart). The distance apart of successive compressions (or successive rarefactions) is the wavelength of the sound wave (Figure 2.2).

For animals living surrounded by air, feeling and hearing are two distinct ways of sensing the environment, although land-living animals do occasionally experience the two senses as one, when they detect very low frequency sounds (i.e. very deep sounds, of low pitch) travelling through the ground: you have probably heard/felt the rumble of an approaching train; and elephants communicate long distance by deep rumbling sounds which can be detected through the feet of other elephants a long way away. Because water is so much less compressible than air, sound travels about 4.3 times faster in seawater than in air, and for a sound wave of a given frequency (i.e. sound of a given pitch), the wavelength in seawater is about 4.3 times longer than it would be in air. This means that much sound in the sea is 'felt'. The distinction between the two is primarily a matter of the distance from the source of the sound. However close we are to a source of sound (say a drum), we don't feel the movement of the air next to the drum skin, because air is so compressible that the air movement is hardly transmitted any distance. In the ocean, the water disturbance caused by a beating fish tail can be felt some distance from the fish, although the sound waves produced at the same time will not travel as far (i.e. a beating fish tail makes only a very small noise).

For the animals that live there, the ocean is a very noisy place, particularly near the sea-surface: natural phenomena such as rainfall, turbulence, and surface waves (including the 'popping' of air bubbles being churned down from the atmosphere) all contribute, along with sounds produced as a result of human activity (e.g. by ship engines and propellers, sonar, and military activity). In addition to these, there are the noises produced by animals themselves, by swimming and feeding, and communicating with one another.

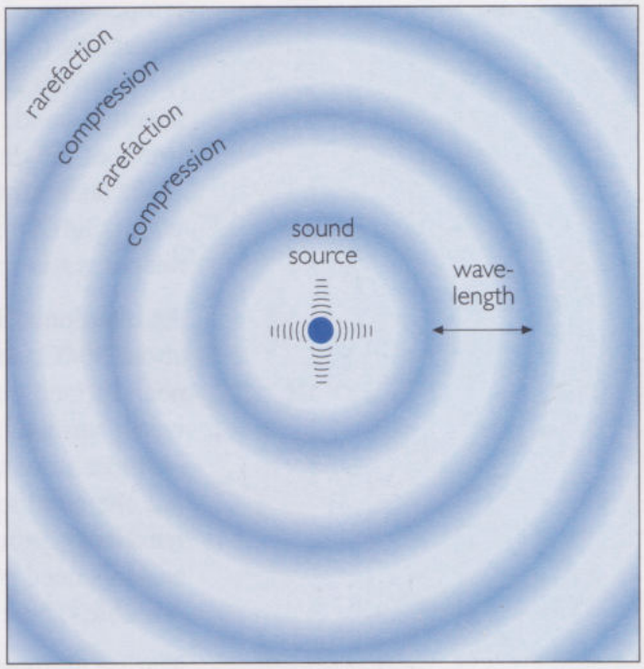


Figure 2.2 Diagram to illustrate the production of sound in a fluid such as air or water. Sound is produced by something that is vibrating: the faster the vibration, the higher the frequency of the sound. The larger the amplitude (size) of the vibration, the greater the intensity (loudness) of the sound produced. The sound wave travels out in all directions away from the source, until its energy is absorbed by the surrounding environment. The distance between one compression and another, or one rarefaction and another, is the wavelength of the sound wave. The longer the wavelength, the lower the pitch of the sound.

As sound can travel through seawater considerably further than light, it is used by a variety of different marine organisms for long-distance communication. Over much of the depth range in the oceans, the precise *speed* at which sound travels is determined largely by the pressure exerted by the overlying water, which increases with increasing depth. We will be having a closer look at sound, and the effects of pressure in the oceans, in later chapters.

A final property of water worth noting is that (as we have seen) it is very good at dissolving substances. In fact, it can dissolve more substances and in greater quantities than any other liquid. It is because of this great dissolving power that the sea is so salty.

2.1.2 Living in seawater

There are two important aspects of living in the oceans that we should focus on first, because they affect all marine organisms – the temperature of the surrounding water and its salinity.

Temperature in the oceans

The geographical distributions of all species, both terrestrial and marine, are limited by the temperature ranges within which they can function. In the ocean, the temperature of surface waters generally decreases with increasing latitude, i.e. with increasing distance from the Equator. As you will see in Chapter 5, this simple pattern is somewhat distorted by surface currents, but generally speaking marine species are found in bands which are approximately parallel to lines of latitude. Furthermore, the limits of the distributions of many species coincide with major 'jumps' in temperature – one such jump occurs off Cape Hatteras on the east coast of the USA, where the warm Gulf Stream leaves the continental shelf and turns eastward, moving out into deeper water (cf. Figure 5.10).

As mentioned in Section 2.1.1, water in the oceans very rarely gets warmer than about 30 °C, and although shallow pools on the seashore can get much warmer, even near-surface waters in the tropics are generally no warmer than 32 °C. Below the warm surface layers, much of the body of ocean water is at about 3–4 °C, and at high latitudes in winter and in parts of the deep sea, temperatures may be 0 °C or below. All chemical reactions, including those in living organisms (i.e. biochemical reactions), proceed faster at higher temperatures and slower at lower temperatures, so animals need physiological 'strategies' to ensure that they function as efficiently as possible. There are two basic ways in which they can do this.

Marine mammals and birds regulate their body temperature to keep it at a constant and relatively high level, so as to enable biochemical reactions within their body to function in a relatively stable environment at a relatively high rate. Most marine mammals keep their temperature at about 38 °C. To generate sufficient heat to maintain such temperatures, they generally have a higher metabolic rate than land mammals of similar size.

How do you think being surrounded by ocean water will affect a marine mammal whose body temperature is about 38 °C?

As discussed earlier, ocean water is rarely warmer than 30 °C, and is usually much colder. Marine mammals are therefore nearly always warmer than their surroundings, and so will continually lose heat to the environment.

To minimise this heat loss, marine mammals tend to be well insulated – whales and seals have a thick layer of blubber (subcutaneous fat), while sea-otters and polar bears spend a lot of time keeping their fur fluffed up and well cared for. Marine mammals also have a special kind of 'heat exchanger' blood circulatory system, which reduces heat loss. We will come back to this topic in Chapter 8.

By contrast, the body temperatures of most fish and all subtidal marine invertebrates (i.e. those that are permanently submerged) are determined by the temperature of the surrounding environment, i.e. by the ambient temperature. Thus if their surroundings warm up, so do they; if their surroundings become cooler, they cool down too. An increase in ambient temperature causes metabolic rate to rise, along with the rate at which physiological processes occur. This increased activity could result (for example) in a faster rate of feeding, but could also lead to inefficient use of energy and of reserves that would otherwise be used for growth and reproduction. However, most fish and marine invertebrates inhabit waters whose temperatures fluctuate relatively little throughout the year, and they are able to regulate their metabolic rates so as to optimise the use of energy resources to allow a balance between 'fuelling' of activity on the one hand, and allowing growth and reproduction on the other.

Living in salty water

Living in the oceans means being surrounded by salty water (i.e. water containing a high concentration of dissolved ions). Perhaps because living organisms first flourished in the oceans, the total salt content of the blood and body fluids of most marine invertebrates is about the same as that of seawater of average salinity (although the proportions of individual ions may not match that in seawater). However, in most fish, the salt content of the blood is only about 30–50% of the surrounding seawater. The reason for this is not known, although it may be because fish evolved in fresher coastal waters or estuaries (or because the early oceans generally had a much lower salinity than present-day oceans), and fish enzymes therefore evolved to function best in low-salinity waters.

Having body fluids with a salt content lower than that of seawater has important physiological consequences. Many living membranes are 'semi-permeable', allowing the passage of pure water but not of the materials dissolved in it. During osmosis, as this process is called, water tends to diffuse across the membrane so as to even out the concentrations of ions in the fluids on either side. In the absence of any compensating mechanisms, this results in a continual loss of freshwater from the fish to the surrounding sea (ancient Egyptians used this principle in mummification, drying out bodies by immersing them in natural salt). Primitive fish – sharks and rays – maintain a high concentration of urea (a waste product) to keep their osmotic balance. Other fish (known as 'bony fish', as explained in Chapter 6) drink substantial amounts of seawater, but excrete very small quantities of urine and actively pass dissolved salts out across their gills. Sea turtles, seabirds and marine mammals also have various means of preserving osmotic balance with their environment.

Moving through seawater: why size matters in the sea

The introductory programme shows a magnificent blue whale – the largest animal there has ever been – so this is a good point to consider the issue of size in the sea. Despite its great bulk, the whale moves through the oceans with ease. It is not

hindered by its great mass, because its enormous body (which would crush its bones if it were a land animal) is supported by the water. The resistance of the water is minimised, not only because of the whale's streamlined shape, but because, being large, it has a relatively small surface area in relation to its volume: this is an advantage when swimming because whereas momentum (and muscle power) are proportional to mass, friction between water and skin is proportional to surface area.

There is another reason why it is advantageous for a whale to have a relatively small surface area in relation to its volume.

Thinking back to the section on 'Temperature in the oceans', can you suggest what this might be?

As mammals, whales need to keep their body temperature around 38 °C. This means that they need to minimise heat loss from their skin to the surrounding water, so the smaller this area is in relation to the volume producing the heat, the better.

Water has a low molecular viscosity – this means that it offers little resistance to objects moving through it: examples of liquids with *high* viscosity are treacle and porridge. For (say) whales or fish (or people) swimming through seawater, the viscosity of the water has little effect, and the progress they make through the water is determined by the propulsive force they generate by moving their tail, body or fins (or arms and legs). The smaller an organism is, however, the more important the viscosity of the surrounding liquid becomes. For those phytoplankton that can swim, moving through water is rather like swimming through treacle would be for us.

If we are swimming, we are propelled forward for some distance under our own momentum after each swimming stroke, and would continue moving until stopped by drag (i.e. friction) with the surrounding water. Similarly, after beating its tail, a fish or a whale moves forward for some distance before it needs to beat its tail again. For a small planktonic organism, the surrounding water is so 'thick' that momentum can play no part in its movement; it only moves forward while its swimming apparatus is in action; as soon as it stops actively swimming, it stops moving. For most zooplankton, the viscosity of the water is non-negligible, but to some extent they are able to move forward under their own momentum.

Note that we have been discussing the effect of *molecular* viscosity – the viscosity of the water itself. Oceanographers studying ocean currents are only concerned with 'eddy viscosity', the internal friction (i.e. resistance to movement) resulting from turbulence (random mixing) in the ocean, as this is a thousand (10^3) times bigger.

The graph in Figure 2.3 shows a very approximate relationship between the size of an organism and the speed at which it typically swims.

According to Figure 2.3, roughly what swimming speed would be typical of a blue whale about 30 m long?

If we draw a vertical pencil line up from 30 m (the 'blue whale' marker at the bottom of the graph) until it intersects the purple line, and then draw another line across horizontally from the intersection point until it meets the vertical axis, we can read off a speed of between 10 and 20 m s^{-1}, i.e. about 15 m s^{-1} (see completed graph in Figure 2.3A overleaf). (Don't worry if you found the logarithmic scales confusing: you won't meet any more graphs of this type in the course.)

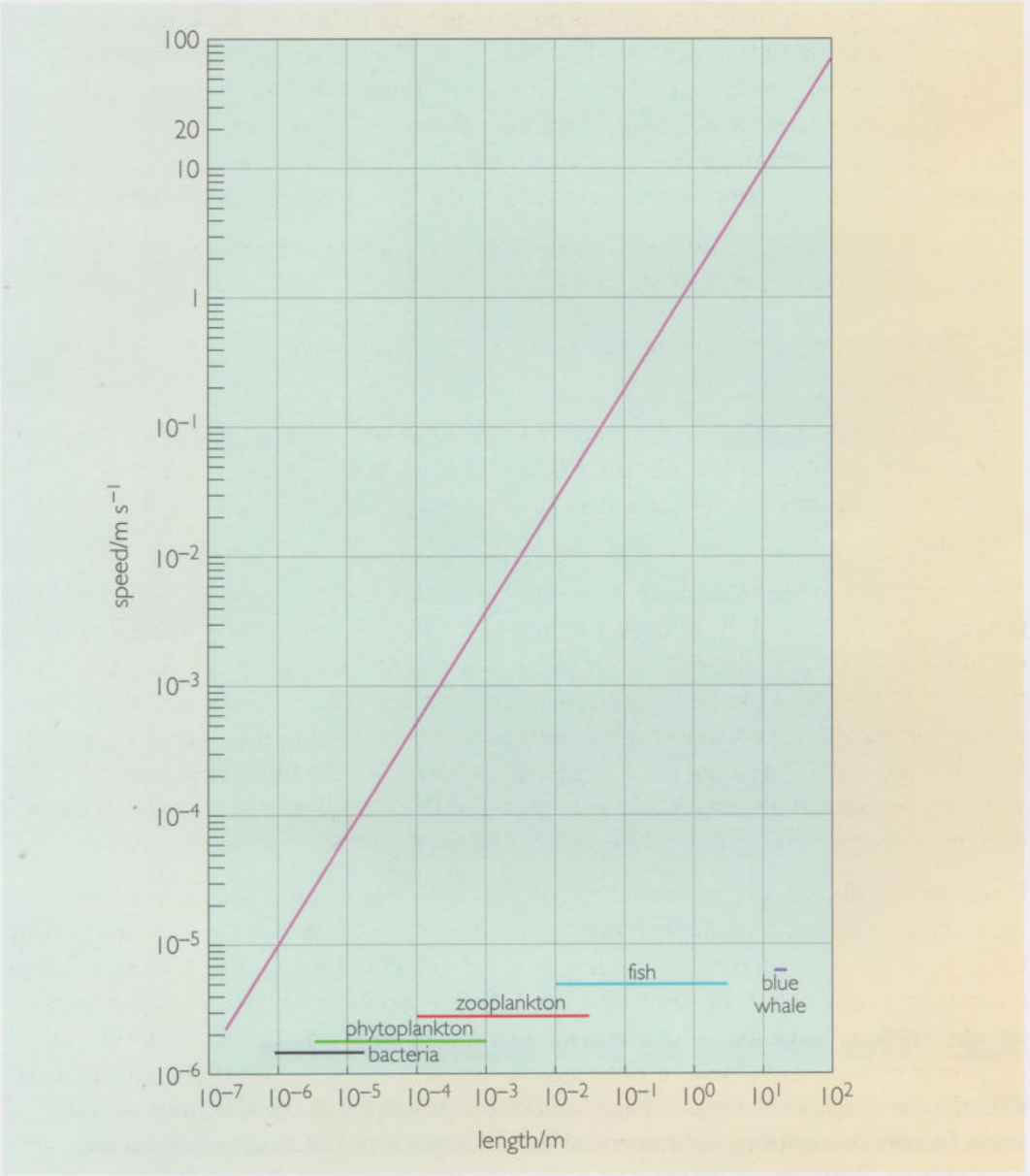


Figure 2.3 Graph to show how the characteristic swimming speed of an organism relates to its length/size. Coloured bars show the size-ranges of different groups of organisms. Because of the large range of numbers involved, scales on the axes are logarithmic, with each major division ten times bigger than the one before. For example, on the vertical axis, the first large tick mark after that for 10^{-6} is for 10^{-5}, which is ten times bigger. The first *small* tick mark after 10^{-6} (i.e. 1×10^{-6}) is for 2×10^{-6}, the next for 3×10^{-6}, etc.

The scientist who obtained the general relationship shown in Figure 2.3 did so by observing an enormous number of swimming organisms, over the whole range of sizes, from bacteria (observed under a microscope) up to whales. He also deduced that in terms of body-length, swimming speeds vary from about ten body-lengths per second for very small organisms, to about one body-length per second for very large animals. It should be stressed that (like the relationship in Figure 2.3) this is only a rough guide; as you will see in Chapter 6, there are a variety of factors which affect how fast a fish (say) can move through the water.

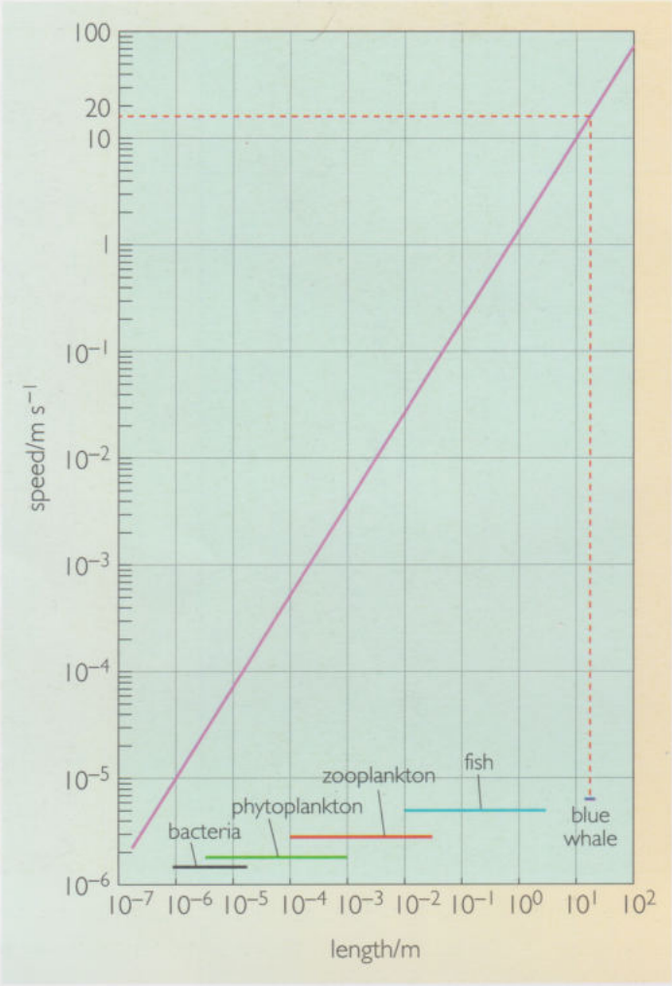


Figure 2.3A Answer to in-text question on previous page. Red dashed lines show how a swimming speed of ~15 m s^{-1} can be read off from the vertical axis, on the basis of a body length of 30 m. (This is only a guide to what the speed of such a whale would be.)

2.2 The shape of the ocean basins

Clearly, the shape of the ocean basins and the topography of the sea-floor are the main factors determining how much of the different types of marine habitat are available as living space. Figure 2.4 shows the topography of the sea-floor represented in three dimensions, with the highest (i.e. shallowest) areas highlighted in yellow (as if lit from the right).

If you have not had much experience in interpreting maps, you should bear in mind that this type of map projection, in which the surface of the spherical Earth is projected onto a flat plane, greatly exaggerates areas of the Earth at high latitudes, and makes high-latitude features that are in reality quite close together look as if they are far apart. For this reason, areas of the map poleward of latitudes 70° N and 70° S have been omitted. Lines of longitude are vertical in this projection and, as on all maps, are determined with respect to 0° (the Greenwich meridian); 180° W, is the same as 180° E.

Take a moment to study Figure 2.4. What features can you make out?

The most obvious feature is probably the enormous mountain chain that snakes down through the Atlantic Ocean. This links up with less well-defined mountain chains in the Indian and Pacific Oceans. Also striking are numbers of arc-shaped depressions, mainly around the northern and western Pacific.

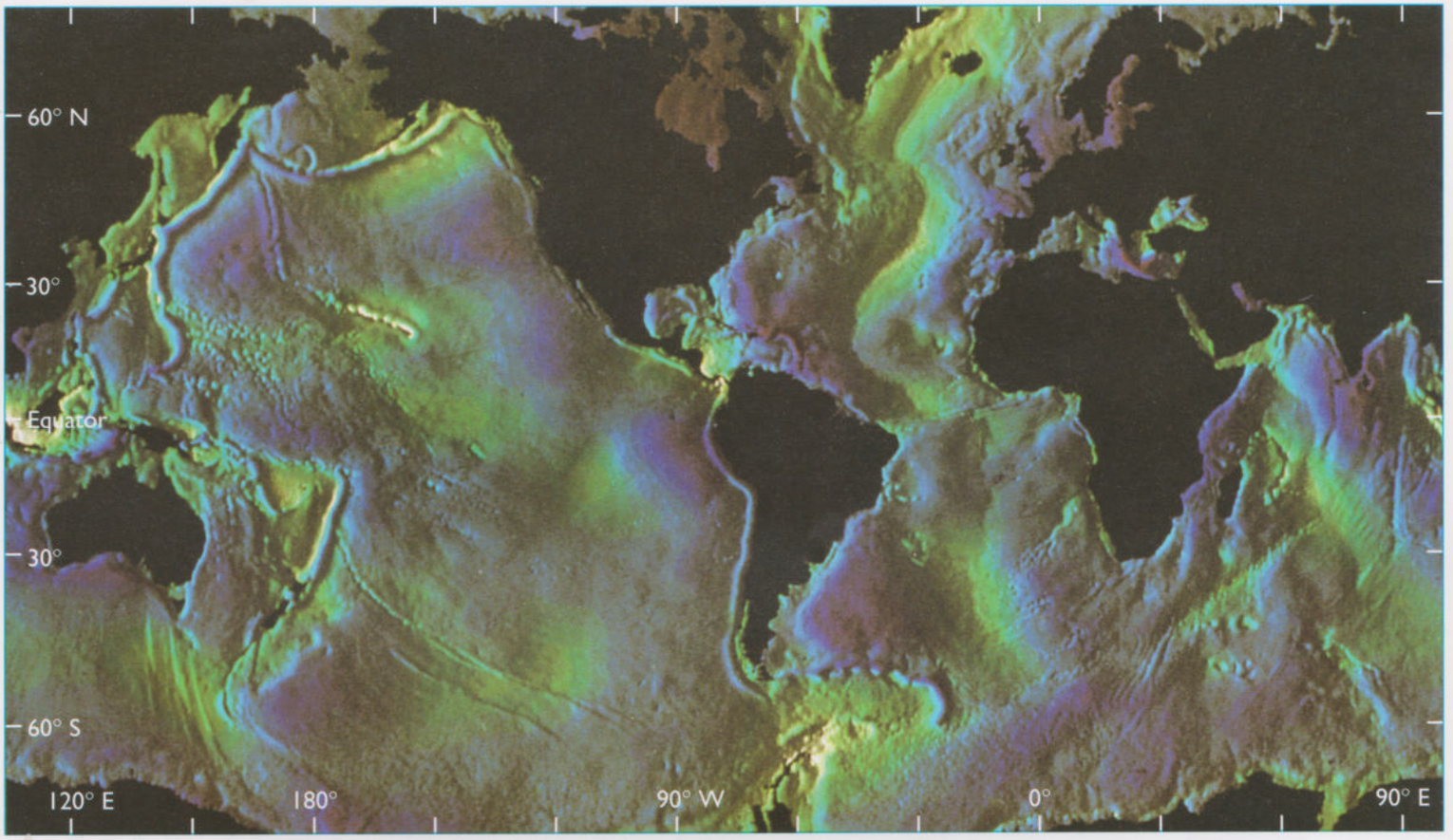


Figure 2.4 Representation of the topography of the sea-floor, shown as if lit from the right. The shallowest areas are highlighted in yellow, and the deepest areas are blue. (This map was made using satellite measurements of the shape of the sea-surface; you need not worry about how this technique works.)

The mountain chain that snakes down through the Atlantic is the Mid-Atlantic Ridge. Hidden in the dark depths of the ocean, it rises over 2 kilometres (km) above the sea-bed, and is part of the longest mountain range on Earth. It is no accident that it seems to follow the shape of the coastlines on either side, and that these coastlines look as if they would fit together like a jigsaw. That is because until about 200 million years ago, there was no Atlantic Ocean. Then, starting first in the north, the continental landmasses began to split apart, roughly along the line of the present ridge, and a new ocean basin began to open. New ocean floor was formed as molten basalt erupted and solidified, and over millions of years the newly formed ocean floor moved away from the central ridge, causing the continents on either side to move apart at a few centimetres a year – about the speed at which fingernails grow. So-called 'spreading ridges' (or 'spreading axes') like the Mid-Atlantic Ridge are also known as constructive margins, because they are the places where new sea-floor is 'constructed' (cf. Figure 2.5 overleaf).

The arc-shaped depressions (around the northern and western boundaries of the Pacific, and in the Atlantic off northern and southern South America) are ocean trenches, which are sites where ocean floor is destroyed. If you study Figure 2.4 carefully, you can see that there is also an ocean trench running down the western side of South America. For obvious reasons, trenches are also known as destructive margins.

So, new sea-floor is continually being formed at mid-ocean ridges, and is continually being destroyed at trenches. The continual formation and destruction of the Earth's

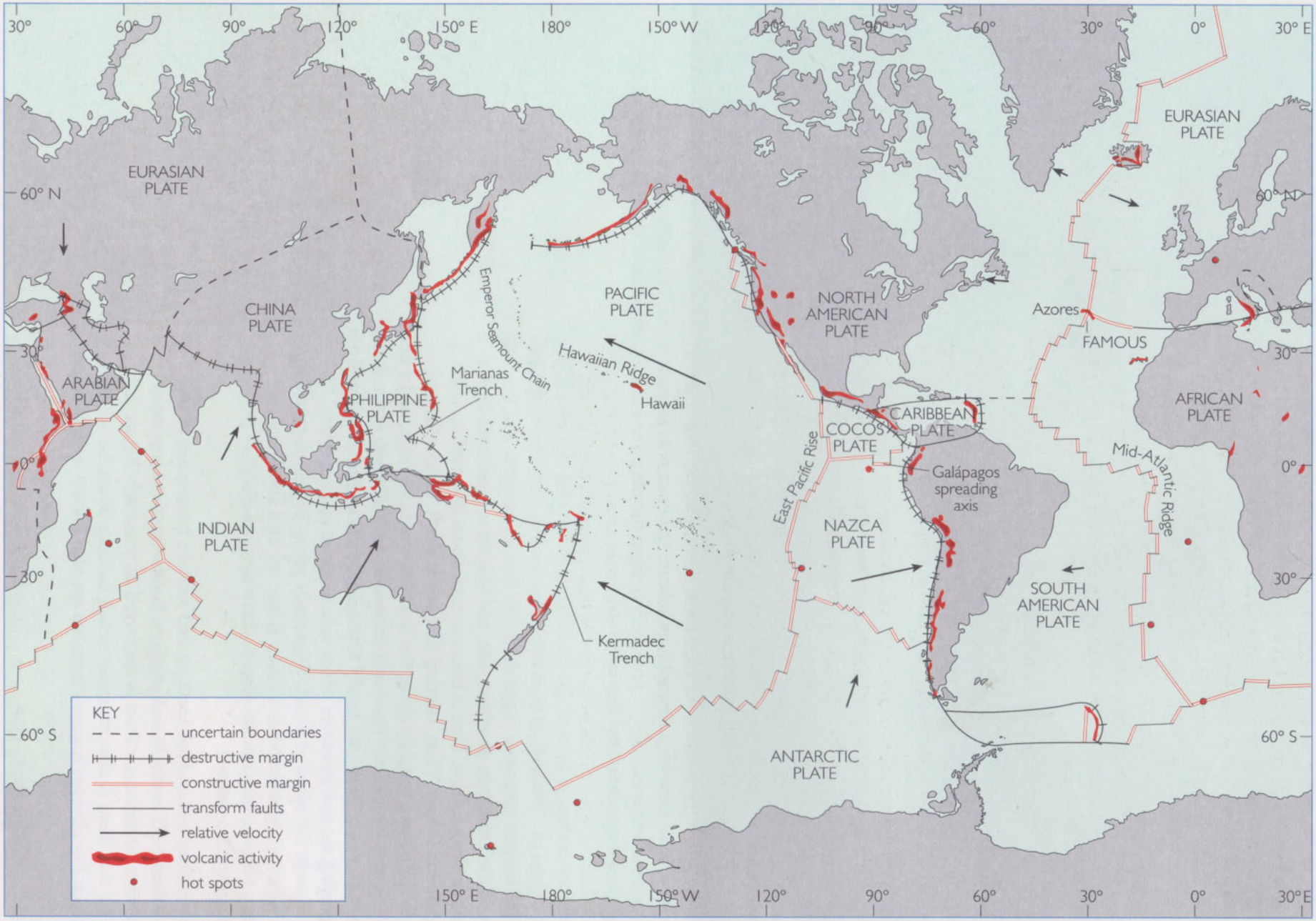


Figure 2.5 The Earth's lithospheric plates, and the boundaries between them. Transform faults are offsets in the mid-ocean spreading ridges; the other types of plate boundaries (see key) are discussed further in the text. Arrows indicate the relative motions of the plates, assuming that the African Plate is stationary; the arrow in the key corresponds to a relative velocity of 5 centimetres per year (cm y^{-1}). Red areas indicate locations of active (or recently active) volcanism (other than that which occurs along spreading ridges – see Figure 2.6). Features and locations that are labell
chapters.

outer layer, or lithosphere (*lithos* is Greek for rock), and the resulting motion of the lithospheric plates over the Earth's surface, is known as plate tectonics. As you can see from Figure 2.5, there are six or seven large lithospheric plates and many smaller ones. Some of these moving plates (e.g. the Pacific Plate) consist entirely of oceanic lithosphere, which is relatively dense; others (e.g. the African Plate) consist partly of oceanic lithosphere and partly of less dense (more buoyant) continental lithosphere. (The term 'crust' is often used instead of lithosphere, especially if the overlying sediments are being included.) Over hundreds of millions of years, the continents move relative to one another. In other words, plate tectonics is the mechanism driving the phenomenon known as continental drift.

Figure 2.6 shows sea-floor being created at a spreading ridge, moving away from the ridge, and being destroyed at trenches. The right-hand side of the diagram shows ocean crust sinking below a continent and being destroyed by melting. This process is known as subduction, so trenches are often called 'subduction zones'. The volcanoes that erupt in the overlying crust are known as 'subduction zone volcanoes'.

The left-hand side of Figure 2.6 shows the result of oceanic lithosphere being subducted below crust that is *also* oceanic. Here, the subduction zone volcanoes form on oceanic crust, and the trenches and the volcanic island chains have the characteristic arc shapes seen in Figures 2.4 and 2.5. Island arcs are common in the western Pacific; indeed, you can imagine the hypothetical cross-section in Figure 2.6 as being a simplified slantwise (north-west–south-east) section across the Pacific, from the Philippines to the coast of South America and the Andes.

Figures 2.4 and 2.5 show that the western Pacific is also the setting for many of the ocean's volcanic islands and seamounts (completely submerged volcanoes) which, like the islands of the volcanic arcs, rise up quite steeply from the deep sea-bed. Many of these islands and seamounts formed when the ocean crust passed over isolated 'hot spots' of volcanism, which from time to time punch through the ocean

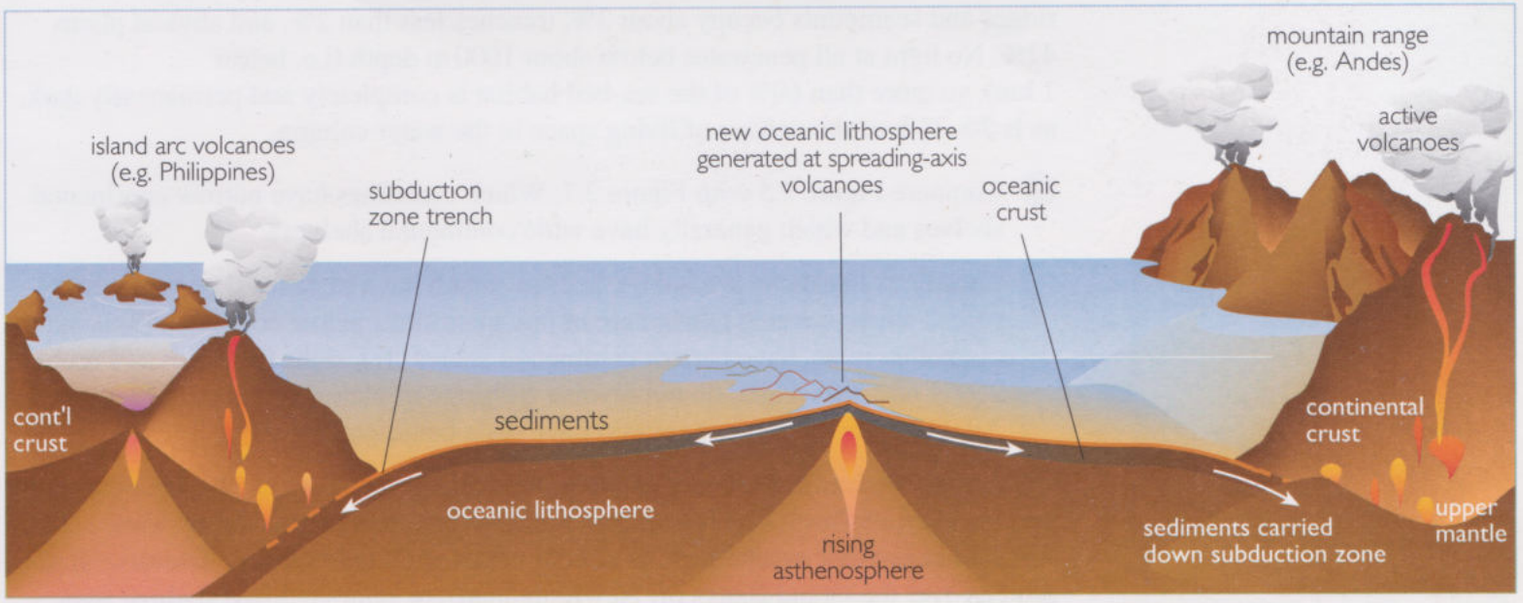


Figure 2.6 Three-dimensional diagram showing the processes associated with the creation and destruction of oceanic lithosphere. New oceanic lithosphere is created by magma (molten rock) rising from below (this underlying layer is known as the asthenosphere). The ridge itself is uplifted because it is warmer, and therefore less dense and more buoyant, than the rocks on either side. However, as the lithosphere moves away from the ridge, it cools, contracts and sinks, eventually becoming covered by a few kilometres of sediment; the arrows show the direction of sea-floor spreading. Note that the vertical scale is greatly exaggerated.

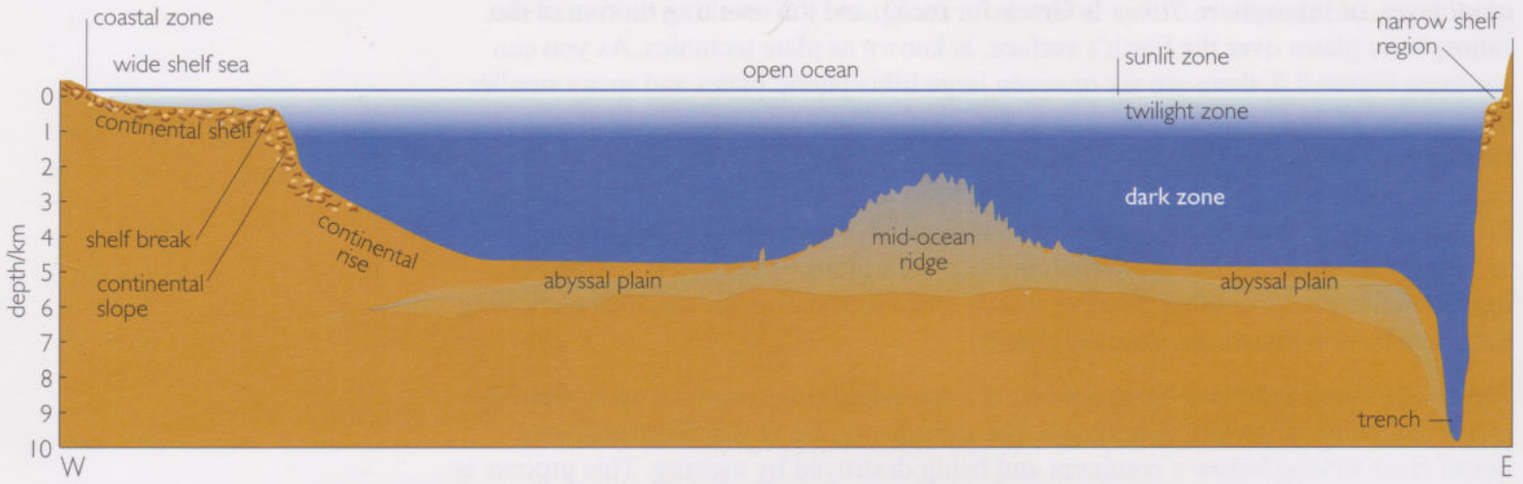


Figure 2.7 Schematic west–east cross-sectional diagram of an ocean basin (i.e. a vertical slice through an ocean basin) showing the main topographic features. The shelf break is the edge of the continental shelf. The speckles on the continental shelf, slope and rise indicate relatively coarse sediments (sand, etc.), which contrast with the fine sediments of the abyssal plains. The depth zones are those referred to in the Blue Planet programmes. *Important:* The vertical scale is greatly exaggerated compared with the horizontal scale, which means that slopes look much steeper than they are in reality.

floor. As you will see, the islands and seamounts produced by volcanism in the oceans (and in some unusual circumstances, the volcanism itself) play a significant role in providing environments that are highly conducive to abundant marine life.

Figure 2.7 brings together information about the general shape of ocean basins and the penetration of sunlight down into the oceans. In a schematic way, it illustrates the distribution and extent of the different marine environments: the coastal environment, shelf seas and the broad extent of the open ocean, with both pelagic and benthic communities. In terms of area, continental margins (shelf, slope and rise) occupy about 20% of the total sea-bed, mid-ocean spreading ridges occupy about 33%, other ridges and seamounts occupy about 3%, trenches less than 2%, and abyssal plains 42%. No light at all penetrates below about 1000 m depth (i.e. below 1 km), so more than 60% of the sea-bed habitat is completely and permanently dark, as is 70–75% of the *volume* of living space in the water column.

Compare Figure 2.5 with Figure 2.7. Which coastlines have narrow continental shelves and which generally have wide continental shelves?

Coastlines like those around the Pacific, which have trenches (i.e. subduction zones) where oceanic lithosphere of one plate sinks below continental lithosphere of another plate, have narrow continental shelves (cf. right-hand side of Figure 2.7). Coastlines which do not involve a change of plate (e.g. those bordering the Atlantic) mostly (but not always) have wide continental shelves.

Continental shelves have a very gentle topography because during the last glacial period, when sea-level was lower, they were eroded more or less flat by wave action. Areas of ocean that overlie regions of continental shelf (particularly extensive areas, such as over the Grand Banks off Newfoundland), or semi-enclosed shallow seas overlying continental crust (such as the North Sea), are known as shelf seas (these are the subject of the Blue Planet programme on 'Seasonal Seas').

In the Blue Planet programmes, the terms 'seas' and 'oceans' are used interchangeably. We will try to use these terms more specifically, using seas to mean 'shelf seas'. (Confusingly, certain enclosed areas, including the Red Sea and the

Mediterranean, are referred to as 'seas', even though they do not overlie continental crust.)

The Blue Planet programmes sometimes use the term 'shallows' to mean near-surface, sunlit water in the open ocean, but it is more commonly used to mean simply shallow water near the coast. Either way, 'shallows' refers to water which is better illuminated and (often, but not always) warmer than deeper water.

Question 2.1 Look again at Figures 2.4 and 2.5. Of which ocean, if any, could Figure 2.7 be a cross-section? ◀

The proportion of ocean area that is shallow sea has fluctuated significantly over geological time. For example, a climatic change that resulted in growth or decline of large ice-sheets, like those that now cover Antarctica and Greenland, would be accompanied by either a fall in sea-level as water was added to the ice-sheet, or a rise in sea-level as the ice melted. This would mean that the area of continental shelf that was submerged would either decrease or grow.

Why would this have important implications for marine organisms?

A growth in the area of continental shelf would mean an increase in the area of relatively shallow water that could be colonised by organisms that prefer shallow, sunlit water – including benthic plants, corals and shellfish beds.

2.3 Shorelines, sediments and the sea-bed

We should now look briefly at the various types of shoreline and sea-bed that are available for colonisation by marine organisms. The characteristics of such *substrates* determine which organisms will be able to flourish in a given area. Seaweeds need rocks for their holdfasts to attach firmly to. Much less conspicuous are the single-celled algae that live on sand grains, and those that form mats on muddy sediments.

Animals that live attached to the sea-bed or move over it – e.g. mussels, corals, sponges and starfish – are known as *epifauna*. Epifauna are particularly abundant on rocky or hard substrates, but are also found on sandy or muddy substrates. Such soft substrates also support animals that burrow. Animals that live partly or wholly within the sediment – e.g. many bristleworms (polychaetes), bivalve molluscs (e.g. cockles), and other invertebrates – are known as *infauna*.

In some unusual circumstances, beaches are made up of debris from living organisms – the best-known example is the coral sand of some tropical islands, but beaches are also sometimes accumulations of shells. Mostly, however, beaches and continental shelves are covered to various extents by sediments derived from the land – that is to say, rocks and boulders of various sizes, sand, silt and mud. These are the products of erosion of the land, including nearby cliffs – not necessarily the ones at the back of the beach in question, but certainly cliffs not so very far away. This is why regions with volcanic rocks have black beaches, and places with limestone or chalk cliffs have pale-coloured beaches. The most common beach material is quartz sand, because the mineral quartz is a major component of the granitic rocks which largely make up the continents.

Under the influence of the elements, rocks erode away – how fast this occurs depends on the type of rock, as you can see from a visit to a churchyard: granite headstones survive much better than headstones carved from softer rocks like limestone. Some of

the constituents of eroded rock are carried away in solution, and will contribute to the saltiness of seawater; the solid fragments will be of various sizes – boulders and pebbles, sand of different grain-sizes and – finest of all – silt and mud. If the environment in which they are initially deposited is subjected to fast-flowing water and/or vigorous wave action, the smaller fragments will be carried away, leaving the larger, heavier ones behind. If the environment is quiet, with only slow currents and/or gentle waves, the smallest particles will not be carried away, and silt and mud carried from elsewhere may have a chance to settle out. Thus, 'high energy' beaches tend to be characterised by lots of exposed rock, with boulders and pebbles, and often sand as well, while 'low energy' beaches tend to have a lot of beach sediment that is silty or even muddy.

Question 2.2 Thinking about the British Isles, can you suggest some good examples of (1) low energy and (2) high energy shorelines? ◀

So, beaches may be rocky and/or sandy; and if there is a sheltered river mouth nearby, or an enclosed lagoonal area, they may also be muddy. The continental shelf may similarly be rocky, sandy or muddy. If it is sandy or muddy, there will be ripples of various sizes on the sea-bed, as well as sand- and mud-banks, and other features, all caused by waves and currents. Several Blue Planet sequences clearly show the sandy nature of much of the continental shelf.

Some continental shelf regions, including parts of the North Sea and the English Channel, have gravelly sediments, which were deposited by glaciers. During the last glacial period, which ended about 11 000 years ago, sea-level fell as much as 100 m below that of the present day. At high latitudes, glaciers extended much further towards the open ocean (as did rivers at low latitudes) and sediments carried by glaciers (and rivers) were deposited on coastal plains that are now submerged continental shelf. Then the ice melted, and the sea once more inundated the shelves, covering the recently deposited sediments of gravel, sand and mud. Eventually, the action of the waves and currents winnowed away the finer sediments – the mud and the sand – leaving behind the gravel.

Continental shelves slope down away from the coast very gently indeed – they have an average slope of only 1 in 1000, or, as an angle, ~0.1° (the symbol ~ means 'about'). The edge of the continental shelf (known as the 'shelf break') has been 'softened' by layers of sediment, and is usually between 20 and 150 m depth (on average, about 130 m depth), although that off the UK is at about 200 m depth. The continental *slope* (cf. Figure 2.7) is much steeper than the continental shelf, on average about 1 in 20 (~ 4°) but sometimes more, as off the south-western British Isles (the South-West Approaches). Part-way down the continental slope, the gradient becomes less steep; this is the start of the continental *rise*, formed from sediment that has been carried down from the continental shelf, often in dramatic flows of water, sediment and rocks known as turbidity currents. Turbidity currents can carve out submarine canyons – gullies in the continental slope and rise – the size of the Grand Canyon. The gradient of the continental rise is about 1 in 100 (~1°).

Note how, in Figure 2.7 (and Figure 2.6), we have had to exaggerate the vertical scale greatly relative to the horizontal scale, in order to show the sea-bed topography clearly. In reality, the oceans are so much wider than they are deep, that their width–depth relationship corresponds roughly to that of the width of a piece of paper compared to its thickness!

In the deep ocean, the continental rise merges imperceptibly into the abyssal plain. Abyssal plains are the flattest and most extensive environments on Earth. Beneath them is the rocky oceanic lithosphere which formed at the spreading ridge millions of years before, covered by the sediment that has been raining down ever since (cf. Figure 2.6). The sediments of the deep sea are fine clay and dust particles carried to the sea by rivers and by the wind, along with organic remains sinking from the sunlit surface layer. The fine-grained nature of the clay and biogenic (i.e. biologically produced) sediment on the deep sea-bed, compared with the coarser sediments of beaches and the continental shelf, can be seen in part II of 'The Deep'. The deep ocean floor generally supports a very sparse fauna, but relatively recently it was discovered that there is an unexpectedly rich diversity of species.

The flat expanses of the abyssal plains are occasionally interrupted by a volcanic island or seamount, whose flanks may support luxuriant communities of animals (as you will see in 'Open Ocean'). In general, however, rocky areas in the deep ocean are rare, although there are areas of exposed rock on the steep sides of the deep ocean trenches. In shallower water, there are of course rocky intertidal zones, as well as those parts of the continental shelf and slope that are scoured by strong currents. In addition, the hard structure that has built up over thousands of years to form coral reefs also acts like a rocky environment (see Chapter 7). And finally, at the spreading ridges themselves, there is the rocky landscape of newly formed ocean floor, yet to be covered with sediment (Figure 2.7). This region mostly has a rather sparse fauna, but at various locations along the ridge, everything changes in the vicinity of hydrothermal vents, where water as hot as 350 °C gushes out of the ocean floor. We will be devoting time to these extraordinary environments later.

Of course, from the point of view of a benthic marine organism, the physical environment it experiences in its day-to-day existence is not only determined by the substrate it lives on and/or in, but on the temperature and other properties of the water in which it lives, by the flow of currents, and the turbulence caused by currents, wind and waves. In the case of organisms that live around the coast, these factors may be continually changing with the ebb and flow of the tides.

▶▶ This is a good time to watch the introductory programme, on DVD 1. We recommend that you begin by watching it all the way through (using 'play all' on the DVD menu). Then, having read the notes below, you can play the programme again or, if you wish, replay individual sequences. (There will be references back to certain sequences later in the course.) ◀◀

Notes on the introductory programme

General note In Chapters 6 and 8, we will look more closely at how fish and marine mammals swim, so you might like to note down any striking aspects of the swimming styles of the blue whale and sealions (both mammals), in sequences 1 and 4, and the marine iguanas (reptiles) in sequence 5. (In later notes, this type of activity will be under a separate heading.)

Sequences 1 and 2 The blue whale feeds by engulfing enormous volumes of water with high concentrations of krill, and then using its tongue and a muscular pouch in its lower jaw to push the water out through the hundreds of overlapping baleen (whalebone) plates that hang down either side of its upper jaw. The krill are trapped on mats of intertwined fibres on the inner edges of the baleen plates. Small fish or squid (perhaps feeding on the krill) may also be

consumed. The expandable grooves in the blue whale's throat, which allow it to engulf such huge volumes of water, mean that it is a type of baleen whale known as a rorqual.

If the whale in the programme was filmed in the Southern Ocean, the krill referred to are Antarctic krill (*Euphausia superba*), which you will meet again in 'Frozen Seas' (Chapter 8). The term 'krill' covers a number of species of shrimp-like zooplankton, known collectively as euphausiids; they are large for zooplankton (up to few centimetres long) and although generally at the mercy of the currents, can swim strongly. Different areas of ocean support different species of euphausiids, and blue whale populations feed on whichever species is abundant in the waters they swim in.

Although we are not providing detailed notes on the various sequences in the introductory programme, we will take this opportunity to say a little about marine reptiles (which feature prominently in this programme) and seabirds, which appear in a number of programmes. Although we will not be saying a great deal more about them, when they make an appearance you might like to watch out for their different feeding and swimming styles.

Marine reptiles

Reptiles are characterised by their tough outer horny plates or scales. They are cold-blooded vertebrates which lay eggs whose shells are tough enough to allow them to develop on land. They have lungs, and breathe air at all stages of their life. (Amphibians, by contrast, typically have soft skins; although they generally live on land, they breed and lay their soft eggs in water; in many ways, the young, which have gills, resemble fish.) In this programme, you will see three types of marine reptiles – marine iguanas (found only on the islands of the Galápagos archipelago), marine turtles and salt-water crocodiles, which live in coastal waters.

Marine turtles usually live in tropical waters, although they may be found at higher latitudes. Green turtles feed on seaweed and seagrasses in shallow water, but all other turtles are carnivorous. For example, leatherbacks (the biggest turtles) consume only gelatinous zooplankton living in the water column, hawksbills feed on sponges, and loggerhead turtles eat sponges, crabs and molluscs. Olive ridley turtles have a wide diet, feeding on jellyfish in surface waters, and diving down to the sea-bed to eat tunicates (sea-squirts), molluscs and crustaceans (e.g. crabs, shrimp and crayfish).

Turtles have been killed for food for centuries, and all eight species are now considered to be endangered as a result of hunting, oil spills, collision with propellers etc., and accidental trapping in fish-/shrimp-catching gear; those that eat jellyfish are at particular risk from accidental ingestion of plastic bags and other floating plastic debris. Olive ridley turtles are relatively abundant, perhaps because of their habit of coming together in mass egg-layings, known as *arribadas* (sequence 9). However, *arribadas* are very convenient for people wishing to harvest turtles and/or their eggs on a large scale, and Kemp's ridley turtles, which are closely related to olive ridleys, and also come together in *arribadas*, are now very rare. We will be coming back to turtles, in the context of breeding migrations, later.

There is only one other type of marine reptile – the sea snake – of which there are 60 species. Sea snakes may come together in schools, and they live in

estuaries, around coral reefs and in open tropical waters. They are extremely venomous, and feed on small fish and squid, which they kill with venom injected by their fangs. Many species lay their eggs on shore, but some give birth to live young at sea.

Shorebirds and seabirds

Like marine mammals and marine reptiles, marine birds (which, like all birds, are warm-blooded) have evolved from terrestrial ancestors. In all, there are about 280 species of marine birds (the exact number depends on how the term is defined). There are two groups of marine birds: shorebirds, which often migrate between two terrestrial sites, winter feeding grounds and spring/summer nesting grounds; and seabirds, which are highly adapted to the marine environment and spend 50–90% of their time at sea.

Shorebirds – including the night herons seen in sequence 8, and the more familiar sandpipers, plover and knot – cannot swim. They mostly feed on muddy, sandy or rocky intertidal zones (discussed in Chapter 3) and have a wide variety of beak types and methods of foraging. The length and shape of the beak are determined by where the bird feeds in the intertidal zone, and by what it eats.

Many species of seabird are as agile under water as above it (Figure 2.8, lower panel). Some plunge into the water to seize zooplankton, fish or squid, some (e.g. pelicans) dive into surface layers, and others (e.g. gannets) plunge to much greater depths. Penguins, murres, puffins and shearwaters pursue their prey underwater using their wings, while cormorants swim after their prey using their feet. (You can see the hunting techniques of gannets and puffins in sequence 12.) There are a great variety of ways in which birds feed at the surface; these include skimming surface organisms from the topmost layer, pattering their feet, dipping, and grabbing food at the surface (Figure 2.8, upper panel).

Many species of seabird nest in colonies of thousands (or even, in some cases, millions) in isolated locations away from predators, but within reach of rich feeding grounds (sequence 11). For reasons that will become clear, there are many more seabirds at high latitudes and temperate regions than there are in the tropics.

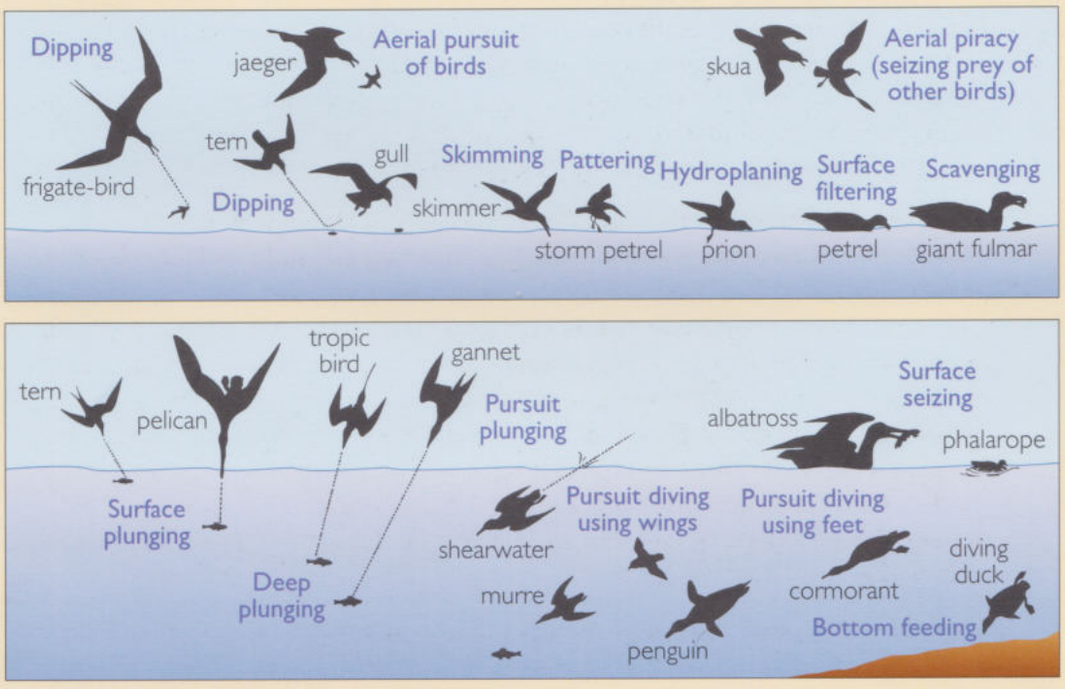


Figure 2.8 The various ways in which seabirds feed, in the air, at the sea-surface and in the water (in most cases, the particular bird illustrated represents just one of a number of bird groups that feed in the manner shown). The best underwater swimmers have short, flipper-like wings (as exemplified by penguins), while birds that fly long distances in search of food (e.g. albatrosses) tend to have long, relatively inflexible wings.

Question 2.3

(a) According to Figure 2.3, what would be the approximate swimming speed of a euphausiid (krill) 1 cm (10^{-2} m) long?

(b) In the introductory programme, we are told that the blue whale can cruise at 20 knots, or about 10 m s^{-1}. Would you say that this speed, and your answer to part (a), are generally consistent with the relationships between body-length and swimming speed mentioned in Section 2.1.2? ◀

Tides

3

The rise and fall of the tide are familiar to anyone who has been to the seaside, but it is not at all obvious that these changes in water level are the result of a kind of wave motion. We will explain what this means later, but first we should look at how the tides are generated.

3.1 What causes the tides?

Most people know that the tides are a result of the gravitational attraction of the Moon acting on the oceans, but the details of how and why tides are generated are not straightforward. The easiest way to begin is to imagine that the Earth is completely covered with water, and that the Moon is directly above the Equator. In these circumstances, the oceans would take on an ellipsoidal (oval) shape, as shown in Figure 3.1, with a bulge towards the Moon and (for reasons that we do not need to go into here) a bulge away from the Moon, and lower water levels in between.

- If the Moon and the ellipsoid of ocean remained stationary while the Earth turned on its axis within the ellipsoid of ocean, how many high tides (bulges) and how many low tides would an observer on the Earth (e.g. on an island near the Equator) experience over the course of 24 hours (i.e. during one complete rotation of the Earth)?
- Over the course of 24 hours, the observer would pass through two bulges, and two 'lows', i.e. they would experience two high tides and two low tides.

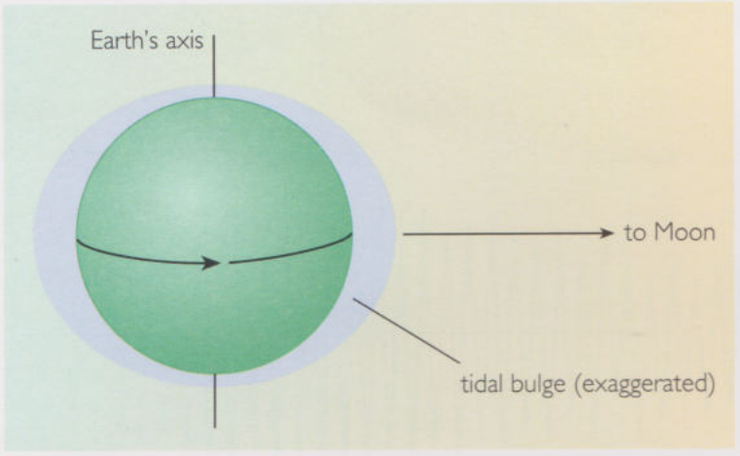


Figure 3.1 The Earth would rotate within an imaginary fixed tidal ellipsoid (shown greatly exaggerated) once every 24 hours. (In reality of course, the ocean cannot take on this ellipsoidal shape because the Earth is *not* completely covered in water.)

In the hypothetical situation just discussed, the Moon and the tidal ellipsoid remain stationary, but because the Earth is rotating, they both move in relation to the Earth. However, the Moon and the tidal ellipsoid do *not* remain stationary, and this affects the timing of high and low tides. While the Earth turns on its axis, the Moon is orbiting the Earth in the same direction that the Earth is turning, making a complete orbit every 27.3 days. As a result, the Moon gets back to the same position with respect to the Earth every 24 hours and 50 minutes (approximately). This is why you will see the Moon reach a particular height in the sky roughly 50 minutes later each successive night, and why the times of high and low tides at many locations are almost an hour later each successive day.

It is not generally appreciated that the Sun also has a significant effect on the tides, and acting on its own would also give rise to two high tides and two low tides a day, with changes in water level about half those resulting from the Moon. It is the combination of the tides caused by the Sun with those caused by the Moon that gives rise to the monthly spring–neap tidal cycle, which is experienced along much of the world's coastlines. Figure 3.2 illustrates how this comes about. The tidal record at the bottom is for a location in the Tay estuary in Scotland, but from the point of view of Figure 3.2 you can consider it to represent the change in water level at any location where the tides show a spring–neap cycle, i.e. one in which tides with a relatively large tidal range alternate with tides with a relatively small tidal range.

Study Figure 3.2, and then check your understanding of what you have read so far in this section by trying Questions 3.1 and 3.2.

Question 3.1

(a) By reference to Figure 3.1 and the top part of Figure 3.2, can you explain why high tides resulting from the Sun alone would be *exactly* 12 hours apart, whereas those resulting from the Moon are 12 hours and 25 minutes apart?

(b) What is the tidal range at the location in the Tay estuary where the measurements were made: (1) at the peak of spring tides; (2) during the smallest neap tides? ◀

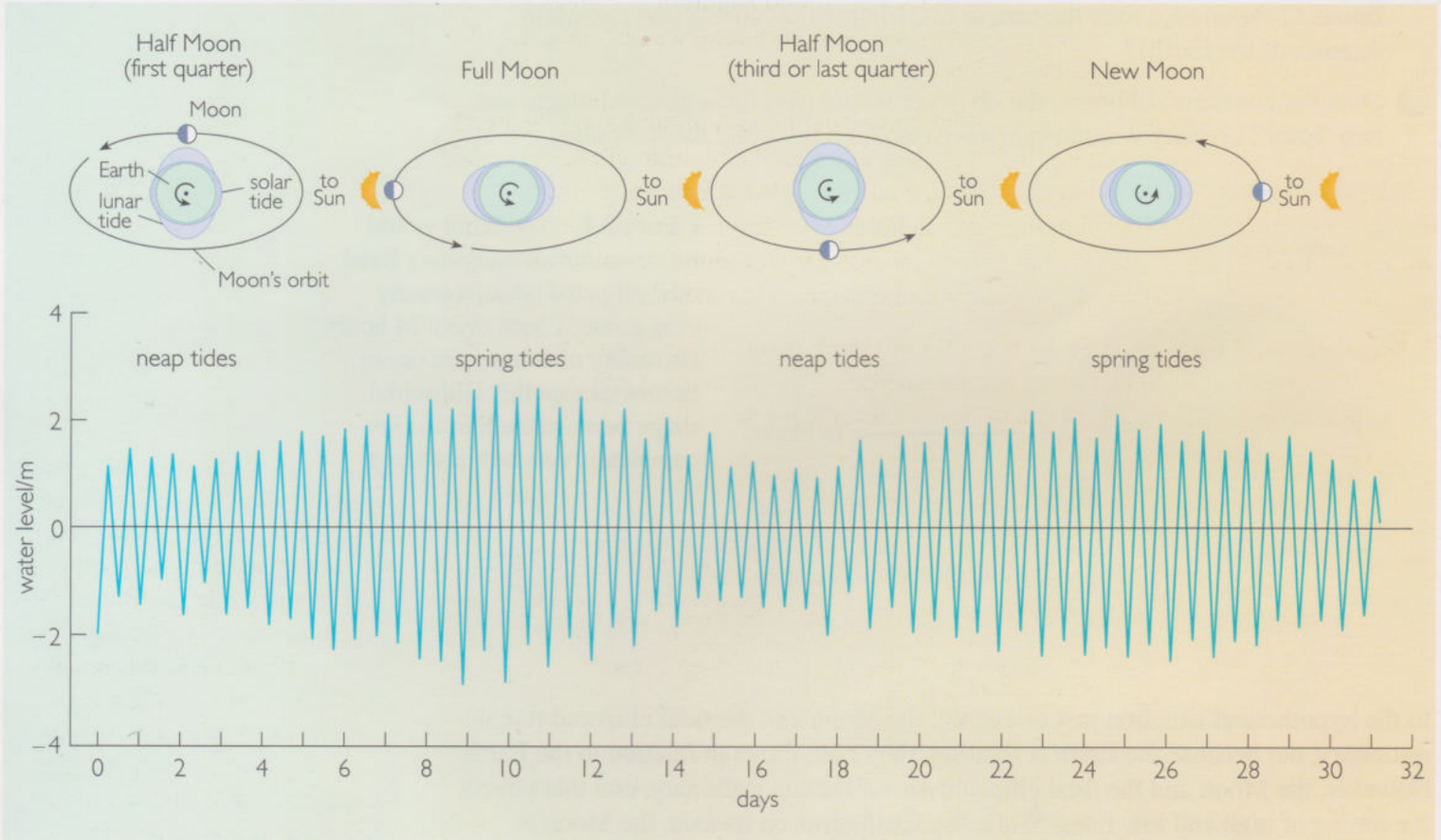


Figure 3.2 Together, the gravitational attractions of the Moon and Sun lead to the monthly spring–neap cycle. When the Moon, Earth (here viewed from above the North Pole) and Sun are aligned, the 'lunar ellipsoid' and the 'solar ellipsoid' combine and there are spring tides (here 'spring' has nothing to do with the seasons); when the Moon and Sun are positioned so that their ellipsoids are at right angles to one another, the result is neap tides. The plot along the bottom shows the resulting variation in water level, with periods of neap tides alternating with periods of spring tides, at a location in the Tay estuary. (The 0-line is mean sea-level.)

Question 3.2

(a) Explain whether the following statement is true or false:

'During the week following a Full Moon, when the Moon is waning, the tidal range will be decreasing.'

(b) When it is New Moon and spring tides for people in Britain, what phase of the Moon, and what part of the tidal cycle, are people in Australia experiencing? ◀

In fact, the situation is not quite as simple as we have been suggesting, because the Earth rotates on its axis much faster than the inertia of the vast mass of the ocean, and friction with the sea-bed, can be overcome. As a result, high tide commonly arrives some hours after the passage of the Moon overhead – a phenomenon known as *tidal lag*. The tidal lag is greatest at low latitudes (where it is about six hours) and has decreased to zero by latitude 65°; the precise lag is always constant at a given location. A further consequence is that, in reality, the biggest spring tides and the smallest neap tides occur a day or two *after* New Moon and Full Moon, and a day or two *after* first quarter and third quarter, respectively.

You may well have realised that tidal flows will be further complicated by the existence of landmasses, which prevent the tidal bulges from travelling directly round the Earth – in fact, the only place where a westward-moving bulge could travel unimpeded round the globe is the Southern Ocean around Antarctica. Instead of travelling around the globe as 'bulges', tides travel as very long waves: the crest of the wave is high tide and the trough is low tide.

Figure 3.3 shows schematically how a tidal wave might travel around a hypothetical ocean basin. The important thing to note is that although the highest and lowest tidal levels are experienced around the coast, the tidal wave also affects the centre of the ocean basin, except for the point around which the wave travels. For reasons which we do not need to go into here, tidal waves generally travel round ocean basins anticlockwise in the Northern Hemisphere and clockwise in the Southern Hemisphere.

Remember that it is only the *shape of the wave* which is travelling around the ocean basin. If you have not studied wave motions before, think of making a rope 'snake' by moving one end from side to side – this causes a wave motion to move along the

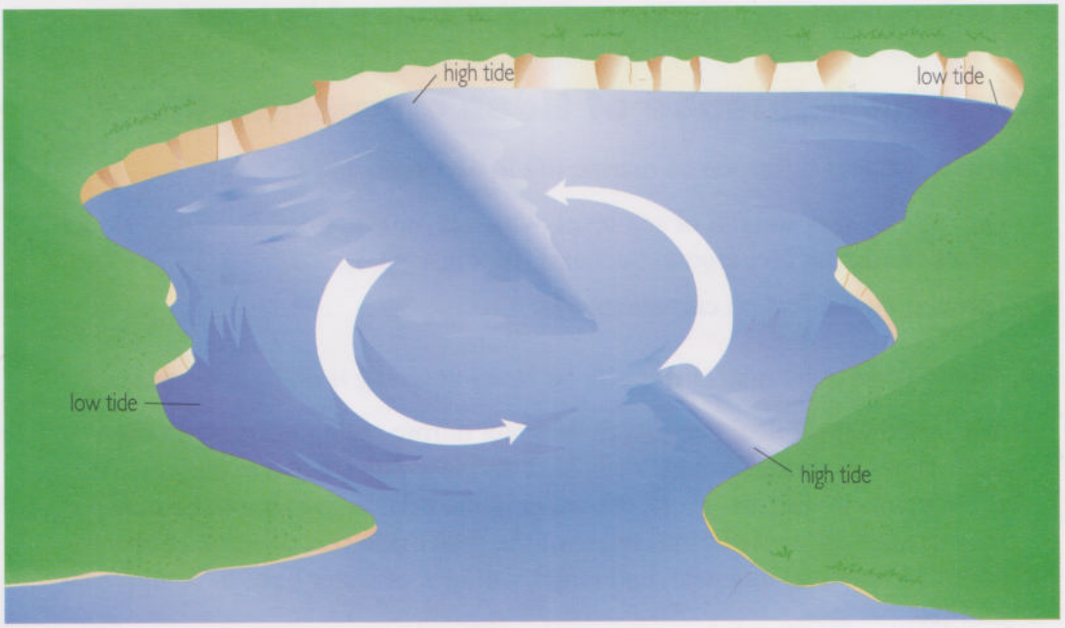


Figure 3.3 Schematic diagram to show how tides travel around an ocean basin as a very 'long' wave, with high tide being the crest of the wave and low tide the trough. This diagram shows a typical situation in the Northern Hemisphere (see text) applied to a hypothetical ocean. (*Note* Not to scale – heights of cliffs are greatly exaggerated; this ocean basin could be anything from a few hundred to a few thousand kilometres across.)

rope, but the rope as a whole remains where it is. The waves generated by wind blowing over the surface of the ocean are similar: although individual water particles describe circular or near-circular motions in the vertical plane, it is the *wave motion* which may travel for hundreds or even thousands of kilometres across the ocean, *not* individual water particles.

In the case of tides, high tides are caused by water flowing in such a way as to locally raise sea-level by 'piling up' water, and low tides result when sea-level is lowered by water flowing away again. This to-and-fro (or, in practice, often elliptical) movement of water is what we mean by tidal currents. The part of the tidal cycle when water is flowing to raise the local water level is known as the flood tide, and the part of the tidal cycle when water is flowing to lower the local water level is known as the ebb tide. At any one place, tidal currents change direction during the tidal cycle. When the tide is turning, tidal currents are in the process of reversing and are very weak; this is known as slack water. Tidal currents are usually strongest around mid-tide, i.e. in the middle of the flooding phase and in the middle of the ebbing phase.

Since the Asian tsunami in December 2004, it has become well known that the giant waves often referred to as 'tidal waves' are usually generated by earthquakes and are nothing whatsoever to do with tides. The term *tsunami* is a Japanese word meaning 'harbour wave', referring to the fact that such waves only become visible when they enter shallow water. As we are now all too aware, once in shallow water, they can rear up to great heights and cause enormous destruction and loss of life.

For a number of reasons, predicting the actual tidal cycle at a given location is very complex. For one thing, in addition to the lunar and solar tidal cycles mentioned above, there are other smaller cycles; also, the actual tidal cycle experienced at any place is affected by the shape of the coast and the topography of the sea-bed. Southampton Water, for example, has a 'double high water' (i.e. two high tides separated by a short period of lower sea-level which is still above mean sea-level), while nearby Portland has a 'double low water'. The Mediterranean experiences very small tides, partly because it is largely isolated from the tidal wave travelling around the Atlantic. In some locations, the combined influences of the sea-bed, the inertia of the ocean and the Earth's rotation are so strong that the two tidal bulges effectively combine into one, giving only one high tide and one low tide a day.

3.2 The influence of tides on marine life

Tides have a direct influence on marine life in two main ways:

1 Through the rise and fall of sea-level, which is most noticeable, and has most effect on marine life, around the coast (cf. Figure 3.3).

2 Through their effect on current speeds.

Would you expect tidal currents to be faster at spring tides or at neap tides?

We would expect tidal currents to be faster during spring tides, when the differences in water level between high and low tide are at a maximum. At these points in the tidal cycle, the water in the tidal 'wave' has to be transported over greater distances in the course of the tidal cycle (i.e. over the course of about 24 hours 50 minutes), and larger volumes of water have to be moved to-and-fro.

3.2.1 Tidal currents

Tidal currents are an important component of the current pattern in shallow waters over continental shelves. Of course, there are also wind-driven currents which are strongest at the sea-surface, and become less strong with increasing depth below the sea-surface.

From what you know about how tides are generated, would you expect tidal currents also to be stronger nearer the surface? (Ignore the effect of friction with the sea-bed.)

No. There is no reason why the motion of water in a tidal wave should be stronger at the surface than deeper in the water column.

At a given point on the Earth, all the water molecules, wherever they are in the water column, will be equally under the influence of the Moon's gravitational attraction. For this reason, there are tidal currents even in the deep ocean.

Locally, the speed of tidal currents is affected by the bottom topography, and especially by the constraining effects of islands, narrow straits or headlands. Water is almost completely incompressible, so the volume of water flowing *into* a given space over a given time has to be the same as the volume of seawater flowing *out* of the space over the same time. So, if a flow of water is forced to become narrower, it will speed up. You may have used this principle yourself to increase the strength of the jet of water coming out of a hosepipe – the smaller the nozzle of the hosepipe, the stronger the jet. In 'Tidal Seas' (sequence 12), you will see two spectacular examples of powerful tidal currents caused by large volumes of water being forced through narrow channels, in the first case between small islands, and in the second case, in the Nakwakto Rapids.

Waves generated by wind blowing over the sea-surface mix the uppermost layer of water, particularly in winter. Meanwhile, strong tidal currents flowing over the sea-bed generate turbulence in the bottom-most layer. In shallow shelf waters, these two mixed layers meet, so the whole water column is well-mixed. As will be explained in Chapter 4, mixing ensures that there is always a good supply of nutrients for phytoplankton, and this is the reason that relatively shallow water, with fast tidal currents, is often highly productive and able to support large populations of animals.

The extraordinary biological productivity of the waters of the Bay of Fundy between Nova Scotia and New Brunswick (which you will see in 'Tidal Seas', sequence 3) are a result of vigorous mixing by strong tidal currents (particularly at mid-tide) in a region with an exceptionally high tidal range – 15 metres at the head of the bay. The large concentration of photosynthetic pigment in the waters of the Bay of Fundy may be seen towards the top right of Figure 5.10. Highly productive water is found over many continental shelves, including the North Sea and much of the continental shelf to the west of the British Isles (Figure 3.4 overleaf). We will be returning to the topic of high biological productivity in the next chapter, and in 'Seasonal Seas'.

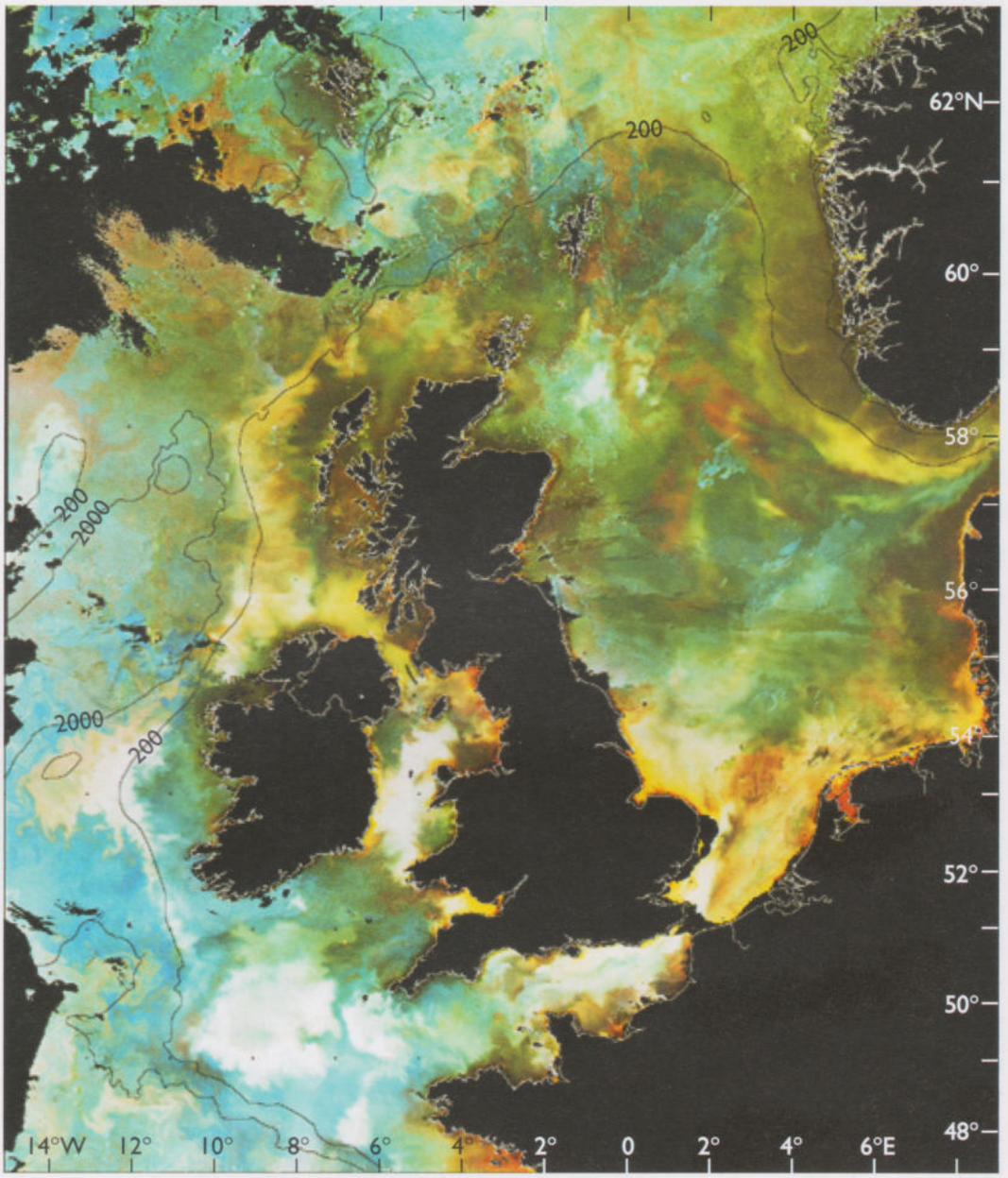


Figure 3.4 Satellite image showing the waters around the British Isles in close to real colour. The 200 m contour corresponds roughly to the edge of the continental shelf. In most of the area on the image, the water colour is dominated by the optical properties of phytoplankton. The pale coloration in the Channel, the southern, shallower part of the North Sea and the Irish Sea is due to particles (sediments, phytoplankton and organic particles) kept in suspension by turbulent mixing. Red coloration along coastlines (particularly those of mainland Europe and north-west England) is caused by high concentrations of sediment. White areas along the edge of the continental shelf, off south-west England, and in the northern North Sea, are probably blooms of coccolithophores (Figure 1.9). Greenish coloration off Norway is the result of the outflow of water from the Baltic, with a large concentration of dissolved organic material.

3.2.2 Zonation

Along any coast affected by tides, the sea-level rises and falls twice every day (or in certain locations, once a day). Below the lowest low-tide mark, the beach/sea-bed is always submerged. Above the highest high-tide mark, there is a zone which is never submerged, but is splashed by spray at high tide – this is sometimes called the splash

zone. Between the high and low tide levels is a zone that is alternately underwater or exposed to the air: this is the intertidal zone.

At any one location, does the intertidal zone always stay the same width?

No, because the daily tidal range is bigger during spring tides and smaller during neap tides.

For this reason, 'tidal range' is often defined as the distance between the high tide level during spring tides and the low tide level during spring tides, both averaged over a long time. (You may see these written as mean high water springs and mean low water springs, or MHWS and MLWS, respectively.)

Will two beaches with the same tidal range always have comparable areas of intertidal zone?

No, because tidal range is distance measured vertically (cf. Question 3.1b). Therefore a gently sloping beach will have a much wider intertidal zone than a steeply sloping beach. (Think of those beaches where you have to walk out for quite some time before being able to swim!)

The Blue Planet series does not look specifically at how organisms are distributed within the intertidal zone, but we can use this environment to look at some principles that apply throughout the oceans. The first of these is the concept of an *ecological niche*. An ecological niche is the combination of conditions – physical, chemical and biological – which characterise the environment occupied by a particular species.

Question 3.3 For a sessile organism – i.e. one that does not move around – living in the intertidal zone, what factors would be important aspects of its ecological niche? Jot down as many as factors as you can think of. ◀

Generally, in a given location, no more than one species occupies exactly the same ecological niche (although species can co-exist if plentiful space is available, perhaps because of predation). As a result, intertidal zones are characterised by vertical zonation – a banding of species occupying successively higher levels above low water mark.

Zonation is particularly noticeable on rocky shores, where it can be seen as horizontal bands of different colours and shades. Figure 3.5 shows examples of zonation on both a rocky shore and a sandy shore, off the coast of North America.

Relatively few animals are permanent residents of rocky shores.

By reference to Figure 1.4, can you say which phylum of animals is best represented in Figure 3.5a?

Phylum Mollusca: periwinkles, mussels and oysters are all molluscs. (Perhaps surprisingly, barnacles are crustaceans.)

Snail-like molluscs such as periwinkles are known as gastropods (gastropod = 'stomach–foot'); most have a single spiral-shaped shell, but some (e.g. terrestrial slugs and sea-slugs) have no shell. The blue mussels and the oysters, which have a pair of hinged shells or 'valves' that can completely enclose the body, are examples of bivalves. Gastropoda and Bivalvia are two classes of the Phylum Mollusca.

Molluscs and crustaceans are the most abundant animals living on rocky shores. Around the British Isles, small periwinkles (*Littorina*) are found near the top of the intertidal zone, with barnacles just below. Then there may be a zone where barnacles

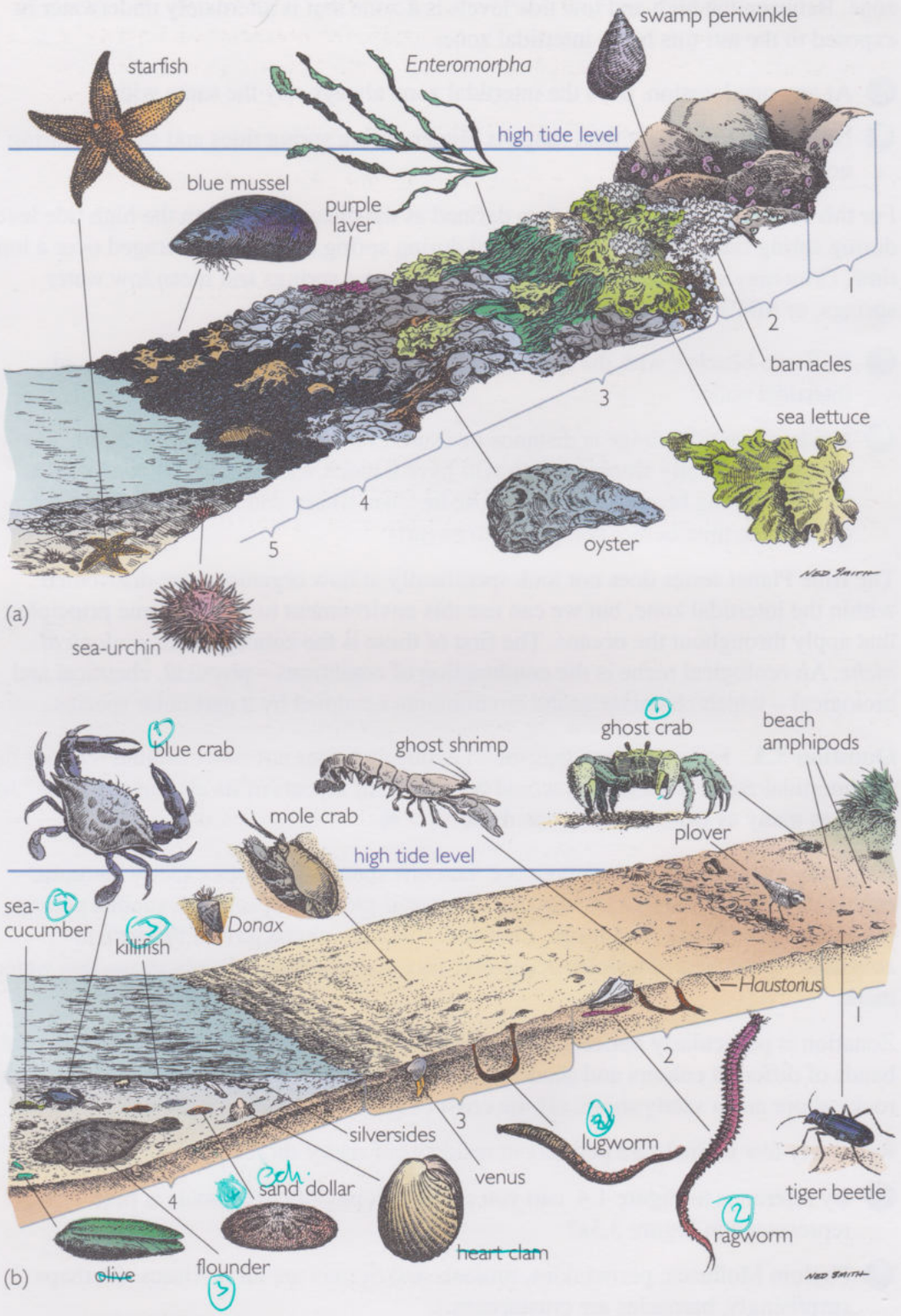


Figure 3.5 Cross-section to illustrate the intertidal zone (a) on a rocky shore (at low tide), (b) on a sandy shore (part-way through the tidal cycle). 1 is the splash zone, 2 the upper intertidal zone, 3 the mid-intertidal zone, 4 the lower intertidal zone, and 5 the subtidal zone (permanently submerged, not shown in (b)). (Note that the examples shown here are North American.)

are found along with mussels, common limpets (*Patella vulgata*), common periwinkles and dog whelks. In the lower part of the intertidal zone may be found blue-rayed limpets (*Patella aspera*), more barnacles, and sea-anemones. Limpets and periwinkles are grazing herbivores. When the tide is in, they move about, scraping diatoms and other small algae from the surfaces of rocks or of larger algae (see below). Apart from the dog whelk, which is a carnivore, all of the other animals

mentioned above feed on plankton filtered from seawater. (We will return to the topic of feeding strategies in Section 3.3.) When the tide goes out, common limpets return to a home site, clamping down tight so that their shells fit into a groove they have worn in the rock. Other animals retreat to humid, sheltered sites under and amongst large seaweeds, in crevices, and under stones.

- In what important way, not so far referred to, does the zonation shown in Figure 3.5a differ from what we often see on rocky shorelines around the British Isles?

- Around the British Isles, seaweeds are usually abundant throughout the intertidal zone.

Light green seaweeds (algae) may be found at all levels, including the shallowest, in tide-pools and on all sorts of surfaces – e.g. stones and limpet shells. They are fairly small, but very fast-growing, and quickly become abundant if there is an influx of nutrients from (for example) sewage effluent. *Ulva* (sea lettuce) and *Enteromorpha* (both shown in Figure 3.5a) are particularly widespread, as is *Cladophora*, also known as blanketweed. Single-celled algae (particularly diatoms) are also found all over the rocky shore.

Unlike the green algae, brown and red seaweeds are generally perennial (i.e. they persist from year to year). On sheltered to moderately exposed rocky shores, the most noticeable organisms are the brown 'fucoid algae' whose main photosynthetic pigment is not chlorophyll but fucoxanthin. These have flexible stems (known as 'stipes') and a flattened leaf-like appearance. The brown seaweed that occurs highest up the intertidal zone is a tough species called *Pelvetia canaliculata*, whose partially rolled up fronds (forming channels), exceptionally thick cell walls, high content of mucilage (a mucus-like substance which reduces water loss, present in all seaweeds) and bushy growth all help it to resist long periods of exposure to the air. One of the best known of the brown seaweeds is *Fucus vesiculosus*, or bladder wrack. Another, *Ascophyllum nodosum* (knotted wrack or egg wrack), only grows in sheltered environments. In very sheltered conditions, it can live for 10 to 15 years, growing in thick masses which completely cover the rocks.

On rocky shores around the northern Atlantic, the commonest seaweed in the lower intertidal zone is another fucoid species, *Fucus serratus* (serrated wrack). Below the low-tide mark grow the kelps (e.g. *Laminaria*), which sometimes form a kind of forest in shallow water. In many parts of the world, rocks below the low-tide mark are covered by red encrusting algae, known as coralline algae, which have deposits of calcium carbonate in their cells. However, not all red algae live this deep – some (e.g. *Porphyra*, from which laver bread is made) may be found at the very top of the intertidal zone.

Seaweed cover produces a whole range of microhabitats which shelter other organisms, including small crustaceans. Larger seaweeds also sometimes have smaller ones living upon them, and these epiphytes (as they are called) are generally thin-walled and therefore attractive to plant-eaters (herbivores). The larger seaweeds may be a direct source of food themselves, and produce large amounts of organic debris, which also forms food for certain animals.

Generally speaking, within the intertidal zone the lower limit of a species' range is likely to be determined by biological factors, such as the presence of predators or competing species. The upper limit is often determined by physiological factors, such

as the organism's tolerance to drying out when exposed to the atmosphere, or to extremes of temperature. Zonation and abundance of species may also be influenced by how easy it is for animal larvae or algal spores to settle. In areas exposed to large waves, the various zones are wider than in sheltered areas with a similar tidal range, as splashing extends the zones upwards.

Vertical zonation is also found on sandy beaches and sand and mud flats, but it is not as distinct or as immediately obvious (Figure 3.5b).

3.2.3 Coping with continual change

Because they are exposed for a larger proportion of each tidal cycle, intertidal organisms which live higher up the intertidal zone need to be better adapted to drying out (desiccation) and heating (or, at high latitudes, cooling) than those that live lower down. As far as plants are concerned, useful attributes include those of *Pelvetia canaliculata*, the brown seaweed which grows at the top of the intertidal zone (Section 3.2.2).

More generally, from the point of view of resisting desiccation, do you think it would be better to be a large or small organism?

To resist desiccation, it is better to keep surface area to a minimum. It is therefore better to be large, because the ratio of surface area to volume will be smaller (you may remember this from Section 2.1.2).

However, the reverse is true when it comes to minimising heat stress at low tide, as this is favoured by a larger surface area : volume ratio – small animals lose heat faster than large ones. A balance therefore has to be struck, so that the animal is not so small that it will dry up when exposed to the air, and not so large that it is unable to dissipate heat sufficiently fast through its body surface.

There are other techniques and aspects of body design that enable animals to avoid being overheated by the Sun at low tide. For example, some intertidal animals maintain their bodies at a temperature lower than their surroundings by making use of both evaporation and circulation of body fluids. Colour also plays a role in fitting organisms for their niche in the intertidal zone: lighter-coloured organisms reflect more solar radiation than darker-coloured ones, which can therefore absorb more. Mussels (*Mytilus edulis*), for example, have both light and dark forms, which are genetically determined. Along the Atlantic coast of North America, the dark-coloured form tends to predominate in northern areas, where freezing is a possibility, and the light-coloured form predominates further south where overheating is more likely.

Heat stress and desiccation are particularly problematic for intertidal animals (and plants) that live attached to rocky surfaces, but these difficulties also have to be dealt with by animals living on beaches, and on sand and mud flats. As the tide ebbs, tidal flats and beaches are exposed as water drains away, often leaving the sediment surface looking quite dry. However, below the apparently lifeless expanse are often large populations of animals, including bivalves and polychaete worms, as well as other invertebrates. Many intertidal animals have surprisingly deep burrows, extending perhaps 25 cm or more below the sediment surface. At high tide, the animals may emerge from their burrows, or extend siphons, tentacles or other feeding and respiratory organs to the surface of the sediment. (Some of the small animals that live in/on sandy and muddy sediments can be seen in 'Tidal Seas' (sequences 4 and 5, and sequence 8, respectively).)

While burrowing animals may stay in the moist sand at low tide, others (e.g. mussels and barnacles) trap small volumes of water in their shells, and yet others are simply exposed to the air. These animals face the problem of being unable to take up dissolved oxygen from the water, or get rid of waste materials. A common means of combating a shortage of oxygen at low tide is to reduce the metabolic rate. Some burrowers (e.g. the lugworm, *Arenicola marina*) have oxygen-carrying blood pigments (e.g. haemoglobin) that only release oxygen for metabolic needs during low tide.

Some species have developed the capacity to breathe from the atmosphere. Mussels 'gape' at low tide, and can take oxygen from the air as long as their gills are moist. The tiny sand-bubbler crab, which you can see in 'Tidal Seas' (sequence 4), lives in the upper part of the intertidal zone and spends quite long periods exposed to the air. On each leg, it has a membranous disk that allows it to take oxygen directly from the air, rather than from the water.

Organisms living in estuaries, where rivers enter the sea, are all to a greater or lesser extent affected by the tide. As the tide rises, seawater flows up the estuary, often flooding large areas of mud and sand flats. Because seawater is more dense than freshwater, it may form a kind of wedge which intrudes up the river below the outflowing freshwater, but if tidal currents and/or river flow are strong, the incoming seawater is mixed with the outflowing river water. Either way, estuarine organisms are alternately covered by seawater and exposed to the air, or alternately bathed in fresh river water and salty seawater (or a mixture of the two).

As mentioned in Section 2.1.2, the body fluids of most marine invertebrates are in osmotic balance with the water that surrounds them, but only relatively few of these animals can tolerate the extreme changes that living in an estuary would impose – the salinity at a given point in an estuary can fluctuate between 2 and 30 (undiluted seawater has a salinity of about 34–35). Most freshwater animals are able to regulate their body fluids to keep their internal salt concentration higher than that of the surrounding water, but relatively few could survive in salinities greater than 9. The species that are able to benefit from the sheltered and food-rich environments provided by estuaries are therefore those relatively select few – usually of marine origin – that are able to cope with the changing salinities.

Many crustaceans (e.g. some species of amphipods and the crab *Carcinus*), and the polychaete *Nereis diversicolor* (the ragworm) are, like freshwater animals, able to keep their internal salt concentration higher than that of the surrounding water. By contrast, most of the polychaete worms (e.g. *Arenicola*, the lugworm) and molluscs (e.g. the bivalve *Macoma*, and the snail *Hydrobia*) are able to tolerate considerable changes in the concentration of salts in their body fluids. (*Note* Polychaetes are named after their many bristles, which distinguish them from the oligochaetes (e.g. earthworms), which are effectively smooth. The Polychaeta and Oligochaeta are two classes of the Phylum Annelida (segmented worms, cf. Figure 1.4).)

A number of marine species are capable of rapidly adjusting their osmotic balance to varying salinity. Many fish species can swim across strong salinity gradients – eels, striped bass and salmon are just a few examples that migrate from seawater to freshwater in a few weeks or even days. Many crab species also migrate over large salinity ranges.

At this point, we need to make a short diversion to look at a fundamental aspect of interactions between organisms in the ocean.

3.3 Feeding strategies and techniques

Although it is not specifically discussed in Tidal Seas', at this stage it would be useful to think in a general way about *what* animals eat, and *how* they feed – a subject touched on in Section 3.2.2.

What are the main categories of animal, in terms of what they eat?

The two most obvious categories are herbivore (plant-eater) and carnivore (meat-eater). You may also have thought of omnivore (eater of everything – an animal that eats a wide range of food of various origins – humans and dogs are good terrestrial examples).

As on land, marine herbivores are sometimes divided into grazers, which remove plant material from a surface (e.g. as mentioned in Section 3.2.2, some species of gastropod mollusc scrape algae from rocks), and browsers, which bite off pieces of plant material.

Predators catch their own (animal) food and scavengers live on the food that other animals have not consumed. There is another very large group which also in a way consists of scavengers – the detritus-feeders (or detritivores). Detritus-feeders eat the remains of plants and animals (including the colonies of bacteria which are decomposing those remains), and the debris produced by other animals, either during feeding, or as faecal pellets. Larger detritivores of necessity eat any microscopic flora and fauna living amongst the organic debris. Most detritus-feeders are benthic – i.e. they live on or in the sea-bed. There are five main ways in which they obtain their food.

1 Some, including several types of polychaete worm, have tentacles with cilia (small hairs), which they spread over or through the mud or sand. Particles of food are collected and brought to the mouth by beating of the cilia or movements of the tentacles.

2 Many bivalve molluscs live buried in the sediment and extend long flexible siphons that they move over the sediment surface, sucking in particles like a vacuum cleaner (you can see a siphon in action in 'Tidal Seas', sequence 5). The food items are sorted from the sediment particles within the mantle. (The mantle of a mollusc is the part of the body which encloses the gills; it is the outer layer of the mantle which secretes the calcium carbonate shell.)

3 Some crustaceans, including some crabs and amphipods, sort particles mechanically with their appendages.

4 A number of detritus-feeders, including polychaetes such as *Arenicola* (the lugworm) and some echinoderms, swallow the sediment and digest any nutritious material (including small animals and algae) as it passes through the gut. They then expel the undigested material as a 'cast' on the sediment surface (you may well have seen such casts on recently exposed sand and mud). These detritus-feeding animals are therefore also known as deposit-feeders.

5 Suspension-feeders, as the name suggests, take food particles suspended in the water column. These particles may simply be sucked in, as in the case of cockles (*Cerastoderma*), which have short inflexible siphons and take in sediment and detritus when the sea-bed is disturbed by waves, or by the incoming tide. Particles may also be collected using feathery appendages which are extended out into the water column. Like the other types of feeders described above, suspension-feeders cannot trap food selectively, so animals that consume plankton will also unavoidably take in other particles. For obvious reasons, suspension-feeders are often also called filter-feeders.

Some suspension-feeders, such as shallow-water species of sponges and tunicates, are *active*, using their own energy to push water through a filtering structure. This strategy is only worthwhile where concentrations of suspended particles are sufficiently high to repay the energy costs of pumping. Passive suspension-feeders, by contrast, extend tentacles or filtering 'arms' into the current, relying on it to bring food. This technique is only successful in environments where flow conditions are predictable, and the current is fast enough to bring a sufficient supply of food. Sea-lilies, featherstars and sea fans are passive suspension-feeders, as are some species of polychaetes.

Before moving on, we should say a little about crustaceans, which are not only amongst the most numerous animals living along the shoreline (along with molluscs) but also extremely abundant members of the zooplankton. You have already encountered copepods in Section 1.3 (Figure 1.10), and euphausiids (krill) in the introductory programme.

The Crustacea are a sub-phylum of the Phylum Arthropoda (animals with jointed limbs) which also includes the insects (Figure 1.4). There are more than 40 000 species of crustaceans, most of which are marine. The extremely diverse Class Malacostraca consists of the sub-classes Eucarida and Peracarida. The former includes shrimps, lobsters, crabs, shrimps and euphausiids; the latter includes the laterally compressed (i.e. flat-sided) amphipods (mentioned in passing in Sections 3.2.2 and 3.2.3; they appear in a number of programmes) and mysid shrimps (which appear in 'Seasonal Seas'). The copepods form the Copepoda. The other classes of Crustacea abundant in marine environments are the Cirripedia (barnacles, which appear in 'Tidal Seas'), the Branchiopoda (including brine shrimps, which also appear in 'Tidal Seas'), the Ostracoda (a striking ostracod can be seen in 'The Deep') and the Branchiura (fish lice).

▶▶ This is a good time to watch 'Tidal Seas' on DVD 1. We recommend that you begin by watching it all the way through (using 'play all' on the DVD menu). Then, having read the notes below, you can play the programme again or, if you wish, replay individual sequences. If you prefer to begin the activities during your first viewing, read the 'Activities' paragraph now (but save the remainder of the notes until you have watched the programme all the way though once.) ◀◀

Notes on 'Tidal Seas'

Activities For each animal shown, try to make a mental note of (or jot down) what category of feeder it is (when possible), and what its feeding technique is (remember that you can make use of the 'pause' button). For the sequence about land crabs towards the end, try to think about what the tidal range will be at the time in question, and how this will affect the speed of tidal currents.

Sequence 1 The time-lapse film of the rising and falling tide shows clearly how the width of the intertidal zone is different for different types of shoreline.

Sequence 2

- The Amazon bore is analogous to a sonic boom. The shape and topography of the Amazon estuary are such that the speed of the tidal wave generated is greater than can be freely propagated up the river. As a result, the wave becomes compressed into a short, steep 'shock wave'. The Amazon bore – known also as the *pororoca* – reaches a height of about 5 m. There are many other less spectacular bores, for example in the Trent, Yangtze, Colorado and Elbe. The Severn bore reaches 1–2 m on spring tides.

- At the end of this sequence, the narration states: 'The Moon *does* create strong tides out in the world's oceans …'. As you know, the rise and fall of the tide (or, looked at another way, the progress of the tidal wave; Figure 3.3) does indeed affect the whole ocean. Nevertheless, tidal ranges are greatest, and tidal currents therefore strongest, around the coast.

Sequence 3 Towrds the end of this sequence, the narration states: 'The flowing tide may provide a feast … but before long it will turn.' Of course, tidal currents can cause mixing and high biological production whichever direction they are flowing in. Here, the narration is referring specifically to the situation in the Bay of Fundy, where large areas of food-rich shallow water 'appear' at high tide.

Sequence 4 The small creatures living amongst the sand grains, pronounced 'myofauna', are spelt meiofauna; this means 'creatures of intermediate size', i.e. neither microfauna, which can only be seen properly under a microscope, nor larger 'megafauna' easily seen with the naked eye (e.g. crabs). (Translucent grains of the mineral quartz can be clearly seen here.)

Sequence 8

- At the start of this sequence, the small invertebrates disappearing into the mud include *Corophium* (an amphipod) plus several ragworms and a lugworm (all polychaetes).
- Here you can see beak shapes and feeding techniques of knot, redshank, oystercatcher and curlew.

Sequence 11 As mentioned earlier, barnacles are crustaceans (i.e. the same group as crabs, shrimps and copepods); the ones shown here are *stalked* barnacles, not the barnacles usually seen around the British Isles. Barnacle larvae are planktonic and recognisably crustacean, but the adults live attached to rocks, coral skeletons, shells of other animals, or even whales. About 3 min 20 s into the sequence, you can see barnacles feeding; they do this by sweeping phytoplankton from the water using six modified legs or *cirri* (plural of *cirrus*, meaning a tendril), hence the name of their taxonomic class, Cirripedia. When exposed at low tide, they withdraw into their shell (which is made up of a number of calcium carbonate plates) along with some seawater which prevents them drying out.

Sequence 12

- If you look carefully, you can see the bladders which (at other stages of the tidal cycle) help to hold the bull kelp upright in the water, so that it can receive the maximum amount of sunlight.
- It has been calculated that plants and animals living in typical shallow tidal waters experience the equivalent of hurricane-force winds on land, twice a day. Aquatic life in the Nakwakto Rapids must endure quite a battering! As seaweeds get bigger, they are at increasing risk of having their holdfasts pulled from the bottom by tidal currents and wave motion. To avoid this problem, many species change their shape as they grow, so that they are less likely to be dragged by water flowing over them.

Sequence 13 At the start, 'weak tides' means weak tidal *currents*.

Sequence 14

- As you may realise from Section 3.1, it is *not* generally true that the Moon's gravitational pull is weaker nearer the Earth's Equator.

- Jellyfish are classified as plankton even though they can swim, because they cannot make headway against more than a very weak current.
- '… the tide is sweeping the whole swarm towards the Bahamas …' should strictly say '… tidal *currents* are sweeping …'.

Sequence 15

- Soft corals are corals without a hard skeleton of calcium carbonate. They do not form reefs (see Chapter 7).
- The razor fish are gathering over a seagrass bed. Seagrasses are flowering plants, not algae. They are found in shallow waters with a soft sea-bed, in temperate, subtropical and tropical regions; most species grow in sheltered subtidal areas. The seagrass species *Zostera marina* (also known as eelgrass) is widespread in shallow waters around the Atlantic, eastern Pacific and Mediterranean. The species which dominates shallow soft areas in the Caribbean (as here) is turtlegrass (*Thalassia testudinum*). Seagrasses probably evolved from land plants, and have simple reduced flowers whose pollen is dispersed by water. Seagrass beds are important nursery areas for many species of fish,

Sequence 16 At the end of this sequence, we see sharks and rays using their well-developed electrical sense to hunt for invertebrates buried in the sand; it has been discovered that they can detect the presence of hidden prey even if it is completely motionless. Electroreception may be used effectively in the ocean because seawater has a high concentration of dissolved ions and so is a good conductor of electricity.

Sequence 17

- The statement 'the water starts losing what little oxygen it contained and quickly becomes stagnant' may be a bit puzzling. As discussed in Section 2.1, oxygen is added to surface water by being mixed down into it, and is also produced by photosynthesis. The water in the mangroves is unlikely to be oxygen-rich: it is sheltered and unlikely to have been recently churned up and thus oxygenated; it is shaded by the trees, and so does not support very much photosynthesis; *and* warm water can hold much less dissolved gas than cold water. Furthermore, the oxygen that *is* there will be being used up by respiration, and by the decomposition of leaves and other organic debris. As a result, the sheltered waters among the mangrove trees readily become low in oxygen (i.e. become 'flat').
- Why tides are large (extra-high highs, extra-low lows) at the equinox will become clear in Chapter 4.
- The influence of hurricanes on sea-level will be explained in Section 3.6.

Sequence 18 The Bahamas are in the western subtropical Atlantic (see any atlas). As discussed in the next chapter, the high atmospheric pressure characteristic of the subtropics (Figure 5.1) means that rates of evaporation from the sea-surface are high (especially in shallow or semi-enclosed waters which get very warm; Figure 2.1). The salinity of the seawater that floods the flamingo breeding grounds is therefore relatively high, and as the remaining water evaporates, the dissolved ions come out of solution and form salt crystals. The first crystals to form are those of calcium carbonate ($CaCO_3$), followed by crystals of calcium sulfate ($CaSO_4$, also known as anhydrite),sodium chloride (NaCl), and salts of potassium and magnesium (K and Mg). This order of crystallisation is determined by the relative solubility of the different salts, and the abundance of the various ions in seawater (cf. Table 2.1).

Now try Questions 3.4 and 3.5, which relate to material in 'Tidal Seas'. (You may need to replay some sequences.)

Question 3.4 In sequence 19, about Christmas Island land crabs, we are told that the crabs are breeding at a time of 'Half Moon in November'.

(a) At what stage of the tidal cycle (spring, neap, or in between) do the baby crabs return to the beach from the sea? What is the phase of the Moon at that time?

(b) Why do you think the baby crabs 'choose' this time to return to the land? ◀

Question 3.5

(a) How would you describe the feeding strategy of the surf-riding snails?

(b) Give at least *three* examples of suspension-feeders, shown in 'Tidal Seas'. For each, state whether they are active or passive suspension-feeders. ◀

3.4 Hitching a ride on the tide

'Tidal Seas' contains some sequences of flounder 'hitching a ride on the tide' to travel in to shallow waters. Bottom-dwelling (i.e. demersal) fish populations living in shelf seas often use tidal currents to save energy on much longer journeys – the migrations that they make between their feeding areas and the spawning ground. Plaice living in the North Sea are a good example of this: when the tidal currents are flowing in the appropriate direction, they swim with the current a few metres above the bottom. At slack water, they descend to the sea-bed and remain there during the other half of the tidal cycle (while the tidal currents flow in the other direction). When the tide runs favourably once more, they then ascend into the water column and continue their journey.

Estuarine fish, and invertebrate larvae that need to develop in relatively fresh water, often stay on or near the bottom during the ebbing tide, and move up into the water column during the flood tide. This technique prevents them from being flushed out of the estuary, and in some cases is used to move upstream. Many other invertebrates and fish hatch in estuarine waters, but their larvae and juveniles need to be dispersed into coastal waters to develop. These animals may time their breeding so that the young can use the currents of the ebb tide to carry them out of the estuary.

3.5 Staying put, in spite of the tide

For many organisms living in the intertidal zone, staying put is simply a question of being as strongly attached to a rock as possible, or of being buried safe below the surface of the sand or mud. But what about those animals that do *not* live permanently attached to rocks or buried in the sediment? Many groups of organisms roam around in a particular part of the intertidal zone to which they are adapted – for example, sandhoppers and small crabs scavenging for scraps. How do these animals prevent themselves from being carried away from their home range, into a part of the intertidal zone to which they are not suited?

Sandhoppers are semi-terrestrial amphipod crustaceans which live by consuming algal debris along the strandline (they are the 'beach amphipods' in Figure 3.5b). You may well have seen them occasionally, but during the day they generally stay

buried in the sand along a very narrow zone just above the high-tide mark. At night, safe from birds, they are widely dispersed, foraging on moist sand in the intertidal zone. So how do they know when and where to burrow back into the sand? Sandhoppers are relatively easy to study in the laboratory and it turns out that they have an internal clock, which triggers emergence after dusk but is not dependent on how light or dark it is – which would not in any case be visible from under the sand! The sandhoppers' cycle, like most such internally generated daily ('circadian') rhythms, including that of humans, is slightly longer than 24 hours, but is 'reset' each day at dawn, when they return to the high-tide line to burrow again. It seems that the sandhoppers are able to determine which direction to go as dawn approaches by heading for the light/dark boundary corresponding to the dune/sky horizon.

It might not seem strange that intertidal animals emerge from their burrows or rock crevices when covered by the flooding tide, but how do they avoid being carried downshore by the ebbing tide? For a number of crustaceans that have been studied (e.g. the isopod crustacean *Eurydice pulchra*, a close relation of the woodlouse), the answer seems to lie in the fact that they have an internal cycle which prompts them to emerge and become active only around times of high tide, being safely back in their shelters by the time the tide is ebbing. Another risk faced by intertidal animals is that of being stranded 'high and dry' during times of neap tides. Again, this may be combated by means of a 'modulation' of the tidal activity cycle mentioned above, whereby the periods of greatest activity occur just after New Moon and Full Moon. Possession of one or more internal clocks, whether simply ~24-hour or attuned to the local tidal cycle, combined with 'orientation cues' – e.g. the light/dark boundary corresponding to the horizon – may explain a lot of otherwise mysterious behaviour.

3.6 Tides and weather

In 'Tidal Seas' (sequence 17), there is a reference to a hurricane leading to extra-high tides. As this suggests, the heights of tides around the coast are significantly affected by the weather. When the atmospheric pressure is low (i.e. there is a depression), the weight of the atmosphere acting downwards on the ocean is less, and sea-level is correspondingly higher (this is sometimes called the 'inverse barometer' effect). In fact, a reduction of atmospheric pressure of 1 millibar results in a rise in sea-level of 1 centimetre.

A large rise in sea-level caused by very low atmospheric pressure is known as a storm surge. As low pressure centres are associated with storms and strong winds, the high sea-levels caused directly by the low pressure are very often made even higher by the effect of strong winds driving water onshore. This is why there are often flood warnings for coastal regions when exceptionally low atmospheric pressure is expected. Coastal areas around the southern North Sea are particularly vulnerable to flooding from storm surges.

Hurricanes – also known as typhoons and cyclones – are strong winds blowing around very low pressure centres (sometimes below 920 millibars). The combination of large volumes of water being driven onshore by strong winds, and the local rise in sea-level in response to the extreme low pressure, means that the resulting storm surges can be devastating, both for coastal wildlife and for local human populations, especially if the storm surge coincides with high tide.

Question 3.6

The format of this question is similar to that of some of the ECA questions. We suggest that you write your answer out in full (rather than just making notes), and then compare it with ours.

(a) (i) By reference to Figure 3.2, write a few sentences explaining why high tides were extra-high in August 1999, at the time of the solar eclipse (when the Sun was obscured by the Moon).

(ii) Fourteen days later, what was the phase of the Moon? *Explain your answer in one sentence.*

(b) Sequence 11 of 'Tidal Seas' shows a mother racoon and her kits hunting for crabs at low tide, at a time of spring tides. Explain why the appearance of the bull kelp in the following part about the rising tide tells us that this was *also* filmed during spring tides. What can you say about the phase of the Moon at the time this was filmed? (*Three or four sentences in all*) ◀

Light, life and nutrients

4

Phytoplankton are sometimes called the 'grass of the sea' because, directly or indirectly, they sustain almost all other marine life. As discussed in Section 1.4, because animals cannot build their own organic material, they have to depend on plants, either directly or indirectly. Building living material from non-living 'raw materials' is known as *primary production*.

- What are the raw materials used in photosynthesis?
- They are carbon dioxide (which in the case of phytoplankton photosynthesis is in dissolved form) and water.

For completeness, we should mention that some bacteria are primary producers, and they use other raw materials. The role of this type of bacteria in deep-sea ecosystems will be discussed later in the course.

In Section 1.4, we expressed photosynthesis in terms of the following 'word equation':

$$\underset{\text{(dissolved in seawater)}}{\text{carbon dioxide}} + \text{water} + \text{light energy} \longrightarrow \text{carbohydrate} + \text{oxygen} \qquad (1.1a)$$

(Note that we have now changed the label below 'carbon dioxide' to correspond to photosynthesis in the ocean.)

Carbohydrates are made up of carbon, hydrogen and oxygen, with one carbon atom and one oxygen atom for every two hydrogen atoms; the simplest carbohydrate is glucose, and its chemical formula is $C_6H_{12}O_6$. If we use this formula to represent organic matter in general, and adopt the convention of putting the energy used in the reaction over the arrow, we can write a chemical equation for photosynthesis as follows:

$$\underset{\text{(dissolved in seawater)}}{6CO_2\ (\text{gas})} + 6H_2O\ (\text{liquid}) \xrightarrow{\text{light energy}} \underset{\text{carbohydrate}}{C_6H_{12}O_6} + \underset{\text{oxygen}}{6O_2\ (\text{gas})} \qquad (4.1)$$

Like any other equation, a chemical equation has to balance, i.e. for each type of atom involved in the reaction, there should be the same number on each side of the arrow. In this case, each side has 6 C's, 12 H's and 18 O's. (Don't worry if you are not comfortable with chemical equations – just concentrate on the 'word equation'.)

Figure 4.1 shows the distribution of primary production on Earth, based on data collected by satellite-borne sensors which measure concentrations of the plant pigment, chlorophyll. This map effectively shows how much plant material (i.e. plant *biomass*) is present *on average* throughout the year. It conveys nothing about the *rate* at which the plant material is produced (i.e. *productivity*), and cannot give any indication of seasonal variations at a given location.

Study Figure 4.1.

- Generally speaking, where are the most productive regions of the ocean? And would you say that marine production is limited by low temperatures?
- The most productive regions are along coasts (especially off river mouths), in shelf seas (cf. Figure 3.4) and in the open oceans north and south of about 35° of latitude. There is certainly no indication that marine production is limited by low temperatures – rather the opposite, in fact.

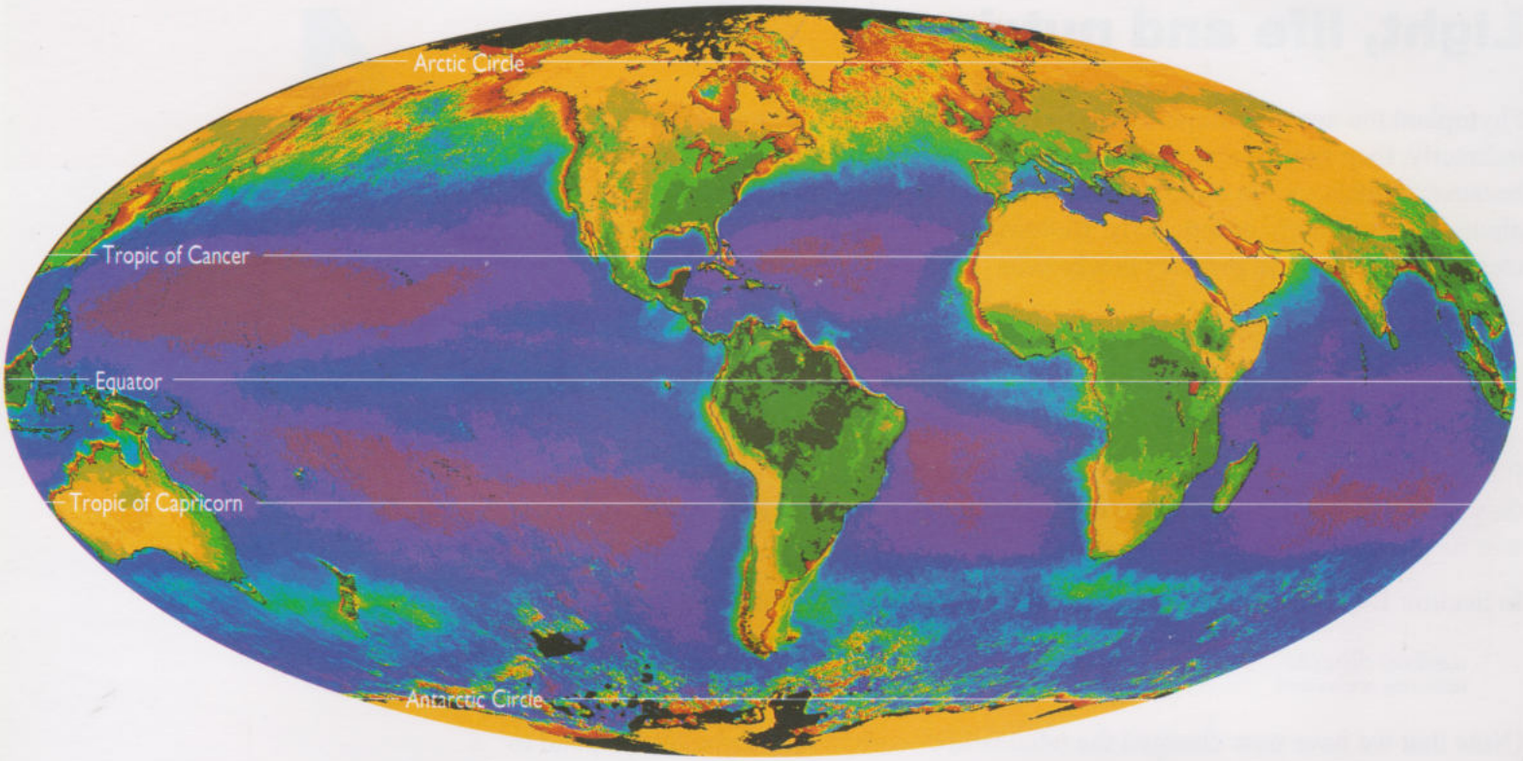


Figure 4.1 Terrestrial and marine plants together make up 99% of the living material on Earth. The map shows the average global distribution of primary production, i.e. plant growth, on land and in surface waters, as indicated by chlorophyll concentration (determined using satellite-borne sensors). In surface waters, regions of highest production are bright red, followed by yellow, green and blue. Least productive oceanic regions are shown purplish-red. (On land, the greatest production is in the tropical rainforests, shown in dark green. The Tropics of Cancer and Capricorn are at 23.4 °N and 23.4 °S, respectively.

The high production of plant material around coasts is partly a result of high concentrations of fertilisers and sewage entering the sea in rivers and in run-off from the land, and is perhaps not surprising. But why should marine production be greater in subpolar regions than it is in the tropics and subtropics? The answer to this will begin to become clear in the next section.

4.1 Why the Earth has seasons

Figure 4.1 strongly suggests that, in the oceans, primary productivity is *not* limited by low temperature. However, as noted above, this map does not tell us *anything* about the effects of seasonal changes in temperature or light levels. Before looking more closely at what these effects might be, let's see why the Earth has seasons at all.

Figure 4.2 shows the effect of a beam of sunlight falling upon the surface of the Earth at low latitudes (near the Equator) and at high latitudes (nearer to polar regions). The intensity of solar radiation at the Earth's surface (on the diagram, the number of rays per unit area) – and hence the surface temperature – depends on the angle of the rays with respect to the surface. The more oblique the rays, the larger the area over which the solar energy will be spread, and the lower its intensity at that location.

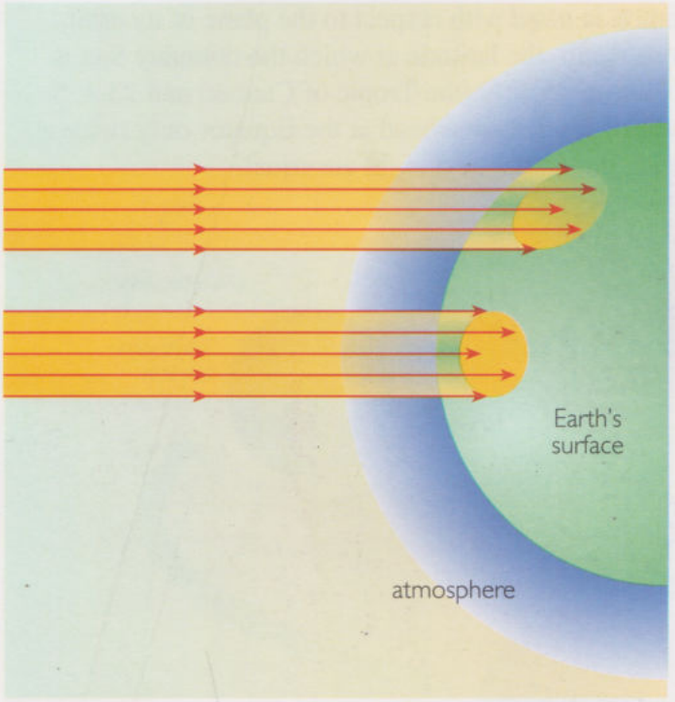


Figure 4.2 Schematic diagram showing why there is a difference in the intensity of solar radiation reaching the Earth's surface at different latitudes.

Bearing in mind that the atmosphere absorbs a proportion of incoming solar energy, can you suggest *another* reason why the intensity of solar radiation at the Earth's surface, and hence the surface temperature, is generally lower at high latitudes than at low latitudes?

The more oblique the rays, the greater the thickness of absorbing atmosphere they have to pass through before reaching the Earth's surface.

If the Earth's axis of rotation were at right angles to the plane of its orbit around the Sun, for any given latitude the angle at which the rays of the noonday Sun fell upon the Earth's surface would remain constant, with higher latitudes in both hemispheres always receiving less solar radiation than lower latitudes (Figure 4.3). The noonday Sun would be overhead at the Equator, and nowhere else. Everywhere on the globe, night and day would each be 12 hours long – there would be a permanent equinox.

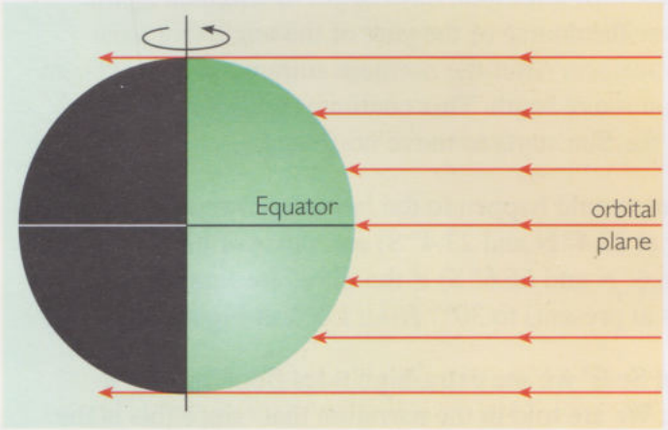


Figure 4.3 Hypothetical situation in which the Earth's axis of rotation is at right angles to the plane of its orbit around the Sun.

However, the Earth's axis of rotation is *tilted* with respect to the plane of its orbit, currently at an angle of 23.4°. As a result, the latitude at which the noonday Sun is overhead continually migrates between 23.4° N (the Tropic of Cancer) and 23.4° S (the Tropic of Capricorn) and back again. It is overhead at the Equator only twice a year, at the equinoxes, when the lengths of day and night are equal.

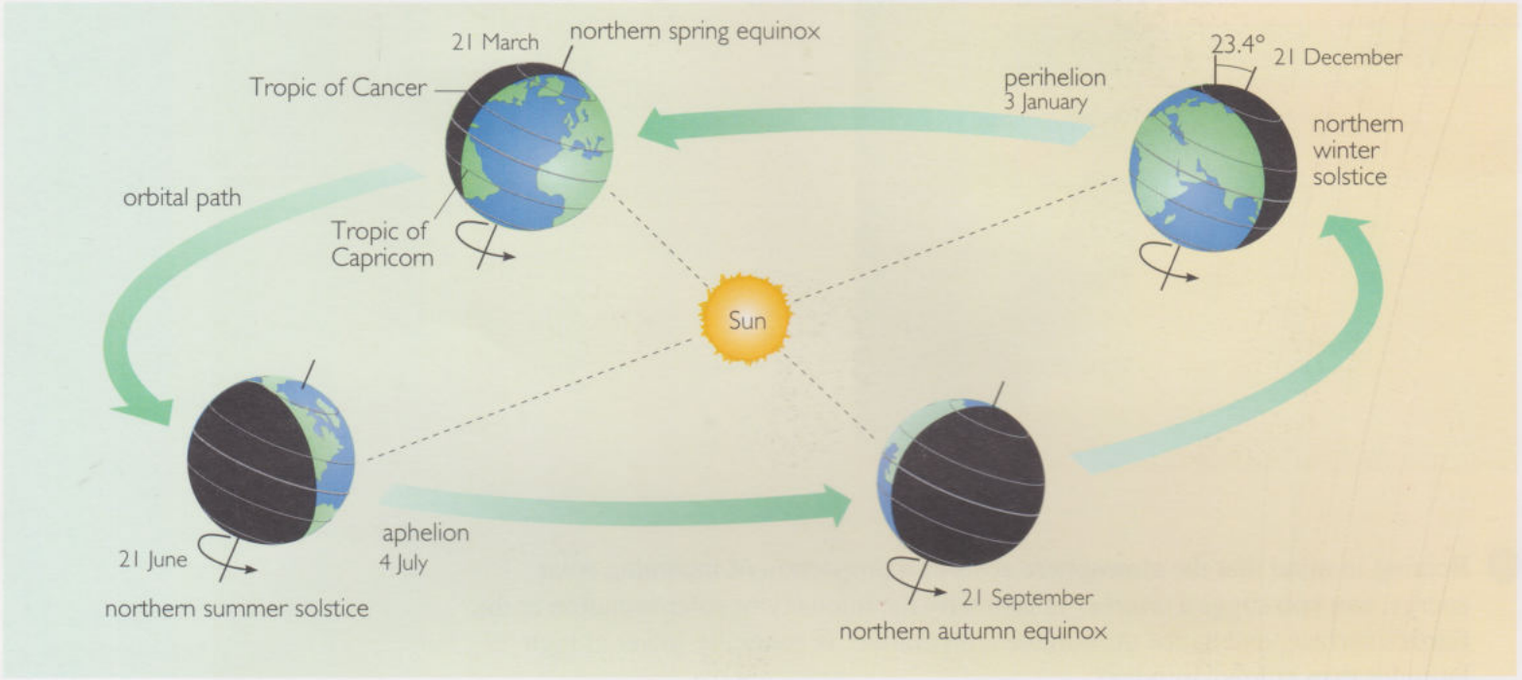


Figure 4.4 The four seasons (here given for the Northern Hemisphere) related to the Earth's orbit around the Sun. The Earth's axis is tilted at approximately 23.4° to a line at right angles to the plane of its orbit around the Sun, with the result that between latitudes 23.4° N and 23.4° S (the Tropics of Cancer and Capricorn, respectively), the noonday Sun will be directly overhead for at least part of the year. When the Sun is overhead one or other of the Tropics, it is the summer solstice (the longest day) in the hemisphere experiencing summer, and the winter solstice (the shortest day) in the other. Poleward of the Tropics, the Sun is never directly overhead.

Figure 4.4 shows the passage of the seasons for the Northern Hemisphere. At the summer solstice (the longest day, 21 June), the noonday Sun is overhead at 23.4° N. Days then get shorter until the winter solstice (the shortest day, 21 December), when the noonday Sun is overhead at 23.4° S; after that, days begin to lengthen again. Figure 4.5b shows the change over the course of the year of the angle that solar radiation makes with the Earth's surface. After the northern summer solstice (1), an observer on the Earth sees the Sun move south. This continues until the southern summer solstice (3), after which the Sun starts to move north again.

Question 4.1 What do you think would happen to the latitudes of the Tropics of Cancer and Capricorn (currently at 23.4° N and 23.4° S) and those of the Arctic and Antarctic Circles (currently at 66.6° N and 66.6° S) if the tilt of the Earth's axis increased from 23.4° (which it is at present) to 30°? *Hint*: Look at Figure 4.5a. ◀

You may remember that in 'Tidal Seas' we see extra-high tides flooding into a mangrove swamp (sequence 17). We are told in the narration that 'since this is the equinox, the tide is rising fast', which suggests that the tidal range is particularly large. As you now know, there are in fact two equinoxes each year, one in the spring and one in the autumn (Figures 4.4 and 4.5).

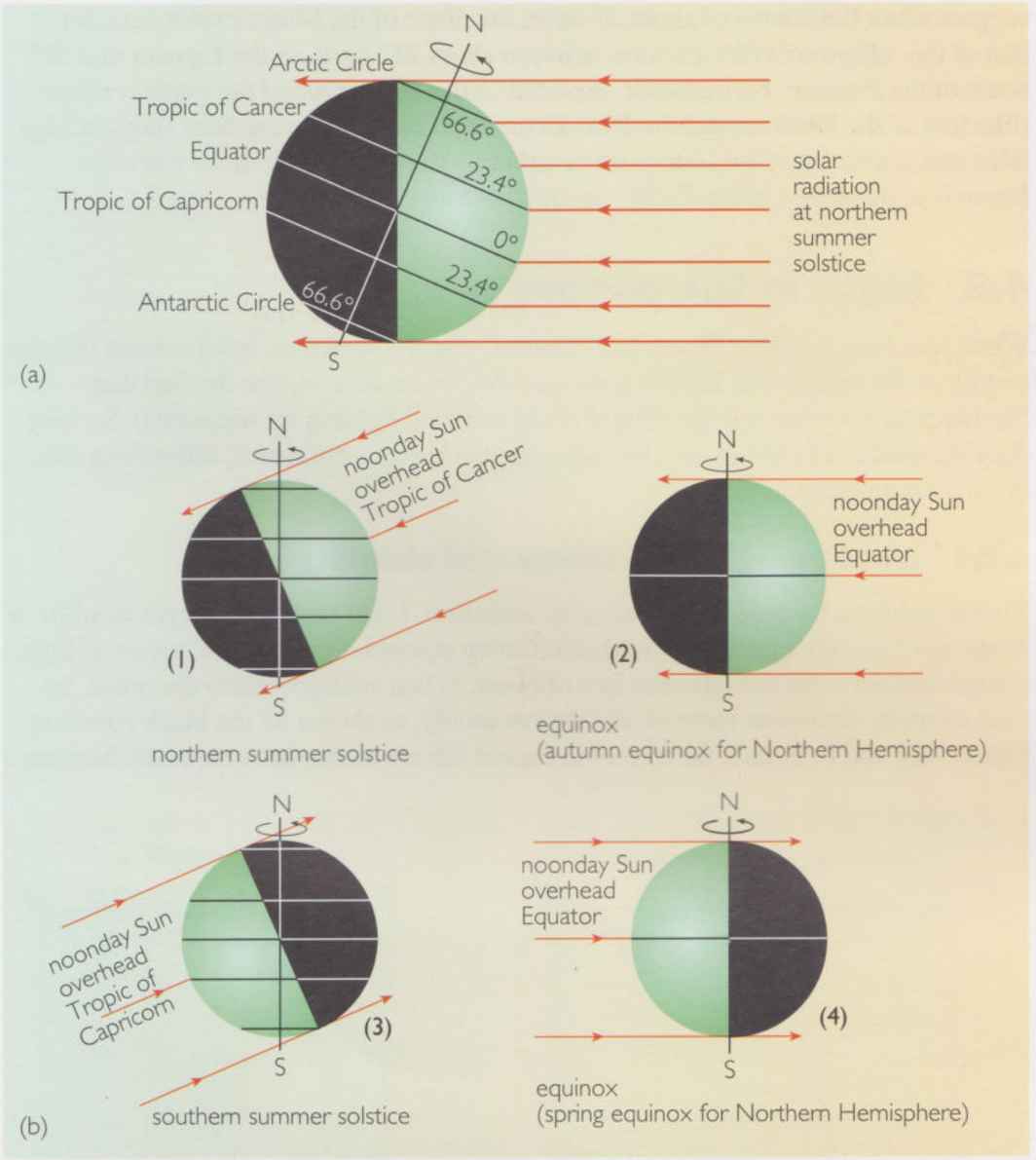


Figure 4.5 (a) The angle of tilt of the Earth's axis (at present 23.4°) determines the latitude of the Tropics (where the Sun is overhead at one of the solstices) and of the Arctic and Antarctic Circles (66.6°, which is 90° minus 23.4°), poleward of which there is total darkness for at least part of the year.
(b) (We recommend you study this in conjunction with Figure 4.4.) The passage of the seasons, shown in terms of the position of the noonday Sun with respect to the Earth. (1) The northern summer solstice, with the noonday Sun overhead the Tropic of Cancer, and (3) the southern summer solstice, when the noonday Sun is overhead the Tropic of Capricorn. In between the solstices are the equinoxes ((2) and (4)), when the Sun is overhead at the Equator, the Northern and Southern Hemispheres are illuminated equally, and days and nights are equal at all latitudes.

So why are tides unusually high around the time of the equinoxes?

At the equinoxes, the Earth is oriented with respect to the Sun in such a way that the Sun is 'above the Equator', so that the gravitational attraction of the Sun aligns with that of the Moon.

However, things are slightly more complicated than this, because the Moon's orbit around the Earth is *not* permanently above the Equator as Figure 3.1 seems to

suggest. Over the course of about 27 days, the plane of the Moon's orbit (and hence that of the 'ellipsoid') tilts, moving between about 28° north of the Equator and 28° south of the Equator. Furthermore, the orbit of the Moon around the Earth is elliptical (like that of the Earth around the Sun) so the most extreme spring tides (highest high tides and lowest low tides) occur when equinoxes coincide with times when the Moon is at its closest to the Earth – a situation known as *perigee*.

4.2 Light in the oceans

While watching the Blue Planet programmes, you will probably have noticed that the quality of the underwater light is quite variable, even allowing for the fact that filming requires relatively good light (even artificial lighting on occasions). So why does the quality of light in, say, the open ocean or over a coral reef, differ from that in, say, a temperate shelf sea?

4.2.1 Light penetration, colour and visibility

Visible light is a form of electromagnetic radiation. Light that we perceive as white is made up of a continuum (spectrum) of different colours – violet, blue, green, yellow, orange and red – the colours seen in a rainbow. When sunlight enters the ocean, its total intensity decreases more or less exponentially, as shown by the black curves in Figure 4.6a and b. In fact, the curves in Figure 4.6 are somewhat unrealistic because

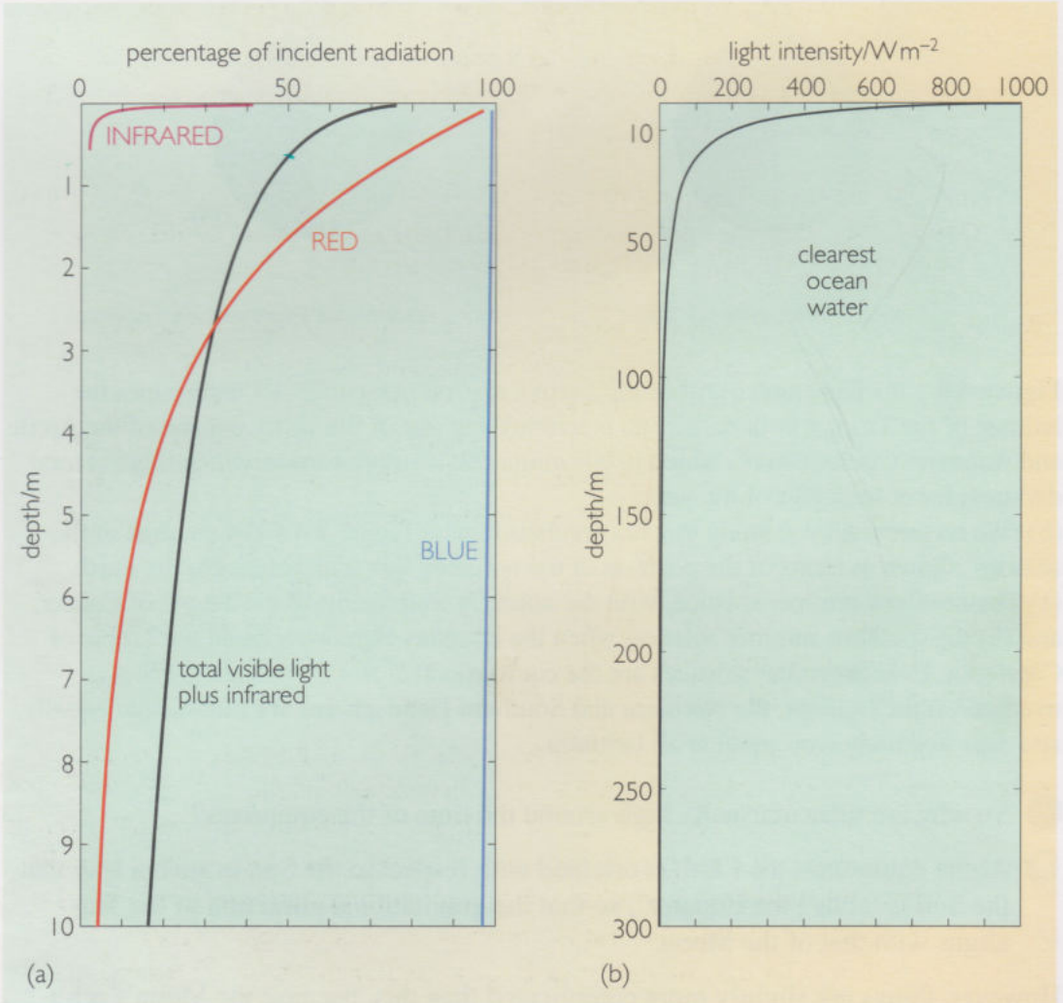


Figure 4.6 (a) Profile showing the variation with depth in the uppermost 10 m of the ocean of total light intensity (black curve), plus profiles for the intensities of red light, blue light and infrared (i.e. thermal) radiation, all plotted relative to their intensity at the surface. These plots have been calculated assuming that the water is clear, and that all of the solar radiation that reaches the sea-surface passes through it, which is not the case (see text).
(b) Profile showing the decline of total light intensity with depth in the uppermost 300 m of the ocean, assuming bright sunlight (an intensity of about 1000 W m^{-2} (watts per square metre) at the surface) and the clearest open ocean water.
(If you are unsure about the use of percentages, or about units of measurement, refer to the *Maths Skills Booklet.)*

they have been plotted assuming that *all* the sunlight that reaches the sea-surface passes through, which of course it does not: some is reflected from the surface, and some is absorbed and scattered by foam, etc. The proportion of incoming sunlight reflected from the sea-surface changes over the course of the day (and with the seasons), because it is significantly greater when the Sun is low in the sky.

The light energy is absorbed by particles in the water column, both non-living (sediment particles) and living (including phytoplankton, which use the light in photosynthesis). Light is also absorbed by seawater itself, and by organic compounds dissolved in the seawater. It is also scattered (deflected 'off course') by multiple reflections from suspended particles; most of the scattering is forward, i.e. the path of most of the scattered light is deflected only slightly from its original direction.

It is important to be clear that the curves in Figure 4.6 show the variation of light intensity with depth *at a single point in the ocean*. This type of curve, often used in oceanographic work, is known as a *profile*.

- According to the black profile in Figure 4.6a, at roughly what depth in the ocean has the total light intensity been reduced to 50% of that incident at the surface? (Ignore the fact that the black profile includes a small contribution from the infrared.)

  (If you need reminding about graphs, practise on this one. Draw a vertical pencil line from the tick mark for 50% down to the black curve. Then, at the point where your pencil line crosses the black curve, draw a horizontal line across the graph until it intersects the vertical axis. You can now read off your answer.)

- Using the method just outlined, we get a value of about 0.6 m, or 60 cm. So, in the topmost 60 cm or so of the ocean, the intensity of sunlight coming down from above is reduced by half.

Question 4.2 Thinking back to both Figures 3.4 and 4.1, would you expect sunlight to penetrate further down through the water column in coastal waters or in the open ocean? Give at least *two* reasons for your answer. ◀

As Figure 3.4 demonstrates, coastal waters may have high concentrations of suspended particles (sediments and phytoplankton) and also tend to have a distinctive colour. Rivers supply high concentrations of dissolved organic ('humic') material produced by decaying plants, and there are also various organic substances produced by the metabolism of plankton. These dissolved organic compounds give coastal (and inland) waters a distinctive yellow–brown coloration, and in older books are sometimes referred to as *Gelbstoff*, which is German for 'yellow substance'. Figure 3.4 suggests how this name arose – the outflow from the Baltic, which has a high concentration of dissolved organic material (but relatively little suspended sediment), looks particularly yellow. By contrast, water in the open ocean is especially clear – the full reason for this will be explained shortly.

Visibility is a matter of contrast – an object may show up against its background because it is a different colour, or because it has a different brightness, or both. An object viewed underwater is seen by means of light rays which travel directly from the object to the eye of the observer. However, like the light coming down through the sea-surface, this will be absorbed and scattered. Furthermore, some of the light from the object will be scattered towards the observer, producing a 'veil of light' behind which the object becomes progressively more indistinct until it disappears against the background.

Except in very shallow water, brightness contrast has a much greater effect on visibility than colour contrast. This is because at depths greater than a few tens of metres, not only has the intensity of the light coming down from above been greatly reduced by absorption and scattering, but the light has become almost monochromatic, i.e. of one colour.

According to the idealised plots in Figure 4.6a, roughly what percentage of blue light passing through the sea-surface penetrates to a depth of 10 m? What percentage of red light penetrates this far?

More than 95% of blue light penetrates to a depth of 10 m, but only about 5% of red light.

Water molecules themselves preferentially absorb light at the red end of the spectrum, and absorb blue light the least. This is why although a small volume of water appears colourless (e.g. in a kitchen sink), a larger volume (e.g. in a swimming pool) looks blue.

Figure 4.7 provides similar information to that in Figure 4.6, but shown in a different way. Here you can see how much of the Sun's energy in different parts of the electromagnetic spectrum (i.e. different wavelengths) penetrates to various depths, while the area under each curve is proportional to the total amount of electromagnetic energy reaching the depth in question. This diagram (along with Figure 4.6a) demonstrates why animals and scenes filmed below a few tens of metres depth always have a blue–green hue, unless illuminated by artificial light.

Seawater also often looks greenish because of the presence of phytoplankton containing chlorophyll. Chlorophyll looks green because it most strongly reflects green light (the middle of the visible spectrum), and most strongly absorbs red light and violet–blue light (at either end of the visible spectrum). There are actually a number of different photosynthetic pigments, of which chlorophyll is the most common. The other photosynthetic pigments absorb light in other parts of the spectrum, and as a result some algae look brown, golden or even red in colour.

Thinking back to Section 3.2.2, does the fact that blue–green light penetrates furthest help to explain why brown seaweeds tend to predominate in deeper water?

Yes. Fucoxanthin, the main pigment in brown seaweeds, absorbs blue–green light most efficiently and reflects light of other colours (which is why these seaweeds look brown).

Subtidal red seaweeds also contain pigments that absorb blue–green light. In fact, red and brown seaweeds *also* contain chlorophyll, but its colour is masked by the other pigments. Presumably the chlorophyll comes into its own at low tide, when the seaweeds are not as deeply submerged. (Interestingly, in very turbid water, it is red light that penetrates the furthest.)

Figure 4.8 summarizes some of the key differences between coastal waters and those of the open ocean, as far as the penetration of sunlight is concerned. From the point of view of life in the upper part of the ocean, the most important point to note in Figure 4.8 is that phytoplankton can grow at much greater depths in the open ocean. The depth zone within which light is sufficient to support the growth and reproduction of plants is known as the *photic zone* (or, sometimes, the

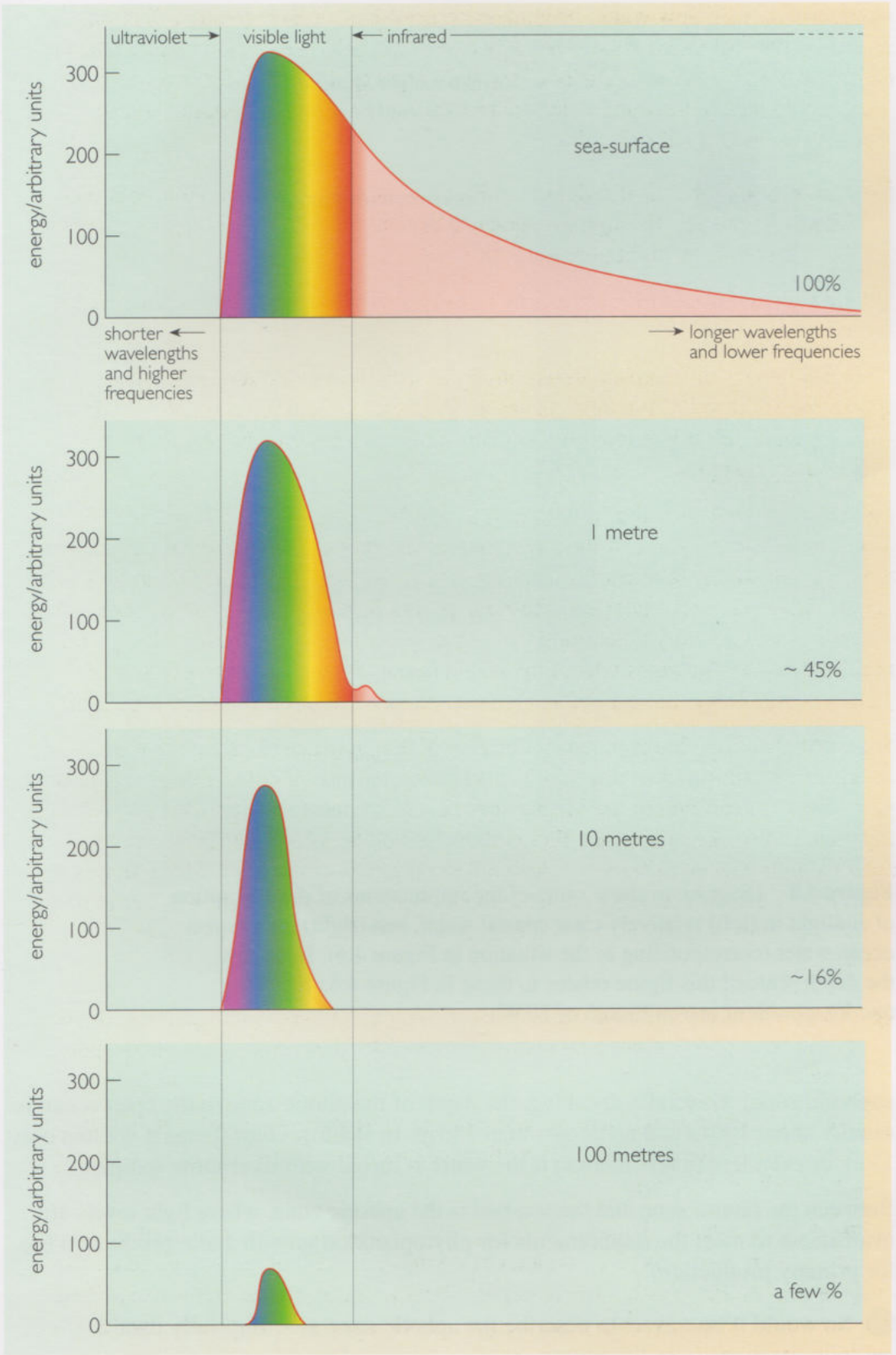


Figure 4.7 Diagram to show how much of the Sun's energy (ultraviolet, visible light and infrared radiation) penetrates to various depths in the ocean, assuming clear water. The top diagram represents the total amount of energy arriving at the sea-surface. Lower diagrams show what percentage of this, and which colours/wavelengths, penetrate to various depths.

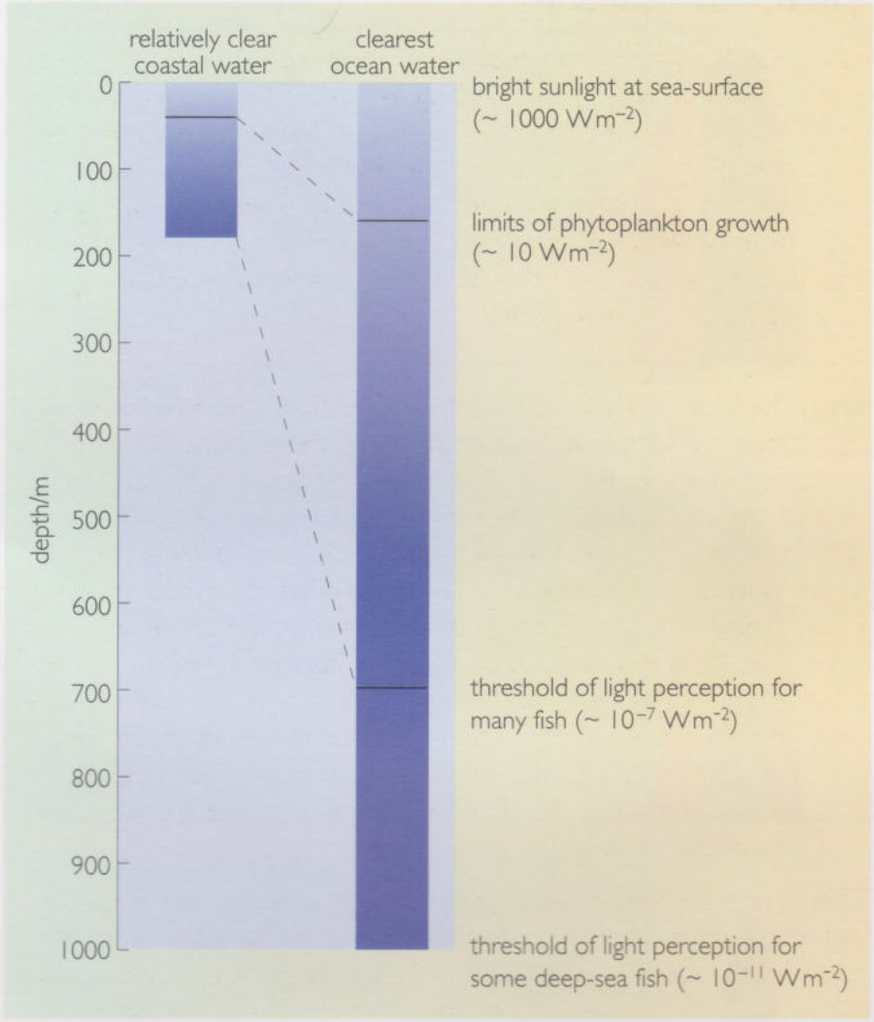


Figure 4.8 Diagram to show some of the implications of the absorption of sunlight in (left) relatively clear coastal water, and (right) the clearest ocean water (corresponding to the situation in Figure 4.6). Note how the depth scale of this figure relates to those in Figure 4.6; 10^{-7} W is one-hundredth of one-millionth of 10 W.

euphotic zone). Generally speaking, the depth of the photic zone in the open ocean is usually about 100 m and no deeper than 150 m. In shallow coastal seas it is often only 15 m, or even less (a few metres) if the water is turbid with riverborne sediment.

Between the photic zone and the sea-bed is the aphotic zone, where light levels are insufficient to meet the requirements for phytoplankton growth and reproduction (i.e. for primary production).

So would it be correct to describe the aphotic zone as 'completely dark'?

No – at least not as far as marine organisms are concerned. Figure 4.8 shows that the very small amount of light that penetrates to about 700 m can be perceived by many fish, and that some deep-sea fish can even perceive daylight at 1000 m depth.

This dim region between the bottom of the sunlit surface waters and about 1000 m depth is sometimes referred to as the 'twilight zone'.

4.2.2 Hiding in the twilight zone

As you will see shortly in 'The Deep' (sequence 2), many animals living in the upper part of the twilight zone remain invisible to predators by being transparent – as indeed do some zooplankton living at or near the surface (including jellyfish, some species of mollusc, and other species related to those that appear in 'The Deep'). For both predator and prey alike, remaining unseen is a great advantage. Another way to avoid being spotted is to be small: with increasing depth, and decreasing light levels, organisms that could be food for predators that hunt by sight can be progressively larger without increasing the risk of being eaten.

Yet another technique for avoiding being eaten is camouflage. A fish whose camouflage techniques have been well studied is the hatchetfish, *Argyropelecus affinis*, which lives at depths where daylight is still important ('The Deep' sequence 3). Like a hatchet blade, it is flat and shiny. Viewed from the front or back, it is slim enough to be barely visible. Viewed from the side, it almost disappears, as the light reflected from its 'mirrored' flanks exactly matches the dark blue of the 'background', which grades downwards into darker and darker blue. Viewed from below, the fish is hard to see because its outline is broken up by blue light from lines of photophores, or light-producing organs, along its ventral (lower) surface. By having one photophore directed upwards into its tubular eyes (which also receive light from above) it is able to match the light being produced by the photophores to that coming down from above. Fine-tuning of the spectrum of light emitted by the photophores to ensure that it exactly matches the ambient light is achieved by means of adjustable magenta-coloured filters over the apertures of the photophores.

This technique of using photophores to break up the silhouette of the body is used by many fish in the twilight zone. It seems a relatively straightforward adaptation, but there are many aspects of bioluminescence that remain mysterious – not least, how it might have evolved in the first place. We will return to this tantalising subject in Chapter 10.

Question 4.3

(a) Why do you think many fish living in mid-depths (i.e. in the upper part of the aphotic zone) have dark upper surfaces but silvery undersides?

(b) Given what you have been reading, especially in connection with Figures 4.6a and 4.7, can you suggest why many animals living in mid-depths have evolved black or red coloration? ◀

The highly directional nature of illumination in the twilight zone has affected the types of eyes that have evolved. Animals that live in the uppermost few hundred metres are likely to need to look out for predators or for food particles coming down from above. As a result, many animals at these depths have eyes that look upwards to some extent (the hatchetfish is an extreme example); others have eyes that look sideways, or nearly so. Planktonic crustaceans often have round eyes, providing equally good vision in all directions. There is not space here to discuss this topic further, except to say that the type of eye an animal has depends on the direction(s) in which it needs to look, and the acuity (sharpness) with which it needs to see. For example, the 'alien creature' *Phronima*, which you will see shortly in 'The Deep' (sequence 2), has double eyes, with a narrow upward-looking field-of-view of high acuity, and a wider lower field-of-view of low acuity.

▶▶ This is a good point to watch part I of 'The Deep', on DVD 1. As usual, we recommend that you begin by watching it all the way through. Having read the notes, you can then play individual sequences, if you wish. ◀◀

Notes on 'The Deep' (part I)

Activity While you are watching, pay attention to the differently shaped eyes, mentioned above.

Sequence 1 Sperm whales are *the* champion divers. You will be able to find out more about how they can dive so effectively in 'Wild Moves: Water', on DVD 2.

Sequence 2

- The nearly transparent 'frilly' kite-shaped animal with long slender antennae, and multiple swimming legs, is *Tomopteris helgolandica*. *Tomopteris* is a planktonic polychaete worm, and is about 25 mm long.
- As mentioned earlier, amphipods are crustaceans. They are distinctive because they are laterally compressed, rather like fleas. 'Amphipod' means 'two types of legs', which distinguishes them from 'isopods', whose legs are all the same (a woodlouse is a terrestrial isopod).
- Most of the 'jellies' seen here are comb jellies, such as *Pleurobrachia* which uses two long tentacles to spread its sticky net. Comb jellies are also known as sea-gooseberries. As this sequence shows, they swim using rows of cilia (fine hairs), reminiscent of those on a gooseberry. As you may have realised from Figure 1.4, comb jellies are closely related to jellyfish, but are classed as ctenophores (pronounced 'tenofours') rather than cnidarians (pronounced 'nydarians'), as they do not have the stinging cells known as 'cnidoblasts' ('nettle cells'), possessed by jellyfish and other cnidarians.
- Siphonophores are colonial cnidarians, in which many individuals with specialised functions are combined to make one organism. At first sight, a siphonophore appears to be an ordinary jellyfish, but closer inspection shows that its 'bell' is made up of numerous compartments. The Portuguese man-o'-war (*Physalia physalia*) is a tropical siphonophore famous for its 10 m-long stinging tentacles.

Sequence 3 You can judge the hatchetfish's camouflage for yourself! Note the use of the magenta filters.

4.3 Heat, light, mixing and nutrients

So far, we have been concentrating on the visible light entering the ocean. Now let's think about the infrared or thermal radiation (i.e. heat). Turn back to Figure 4.6a and study the infrared curve.

By approximately what depth has the intensity of thermal radiation entering the ocean been reduced to 5% of its value at the surface?

Thermal radiation has been reduced to 5% of its value at the surface by a depth of about 0.2 m or 20 cm.

So, thermal radiation from the Sun penetrates into the ocean hardly at all; furthermore, by itself, conduction of heat by water is very, very slow. The way in which heat is carried deeper into the ocean is through *turbulent mixing*. The mechanism for downward heat transport in the ocean is analogous to the method generally used to transport hot tap water from one end of the bath to the other – by stirring! The same is true for water *cooled* at the surface.

The vertical distribution of temperature within the ocean is therefore a result of two main processes:

1 the warming of surface water by the Sun at low and mid-latitudes, and the limited downward mixing of this warm water to form a distinct upper layer, which is markedly less dense than the water beneath; and

2 the extreme cooling of surface water at high latitudes, so that it sinks and then flows equatorward to occupy much of the volume of the deep oceans.

The processes involved in (2) have important implications for life in the deep oceans, and we will be looking more closely at them in Chapter 10. The processes involved in (1) are intimately related to the seasonal cycle of life in the uppermost layers of the ocean, and we will now examine these processes more closely.

In winter, at high and mid-latitudes, storms churn up the surface layers of the ocean (you will see some good shots of this in 'Seasonal Seas'). Because the water is being cooled by cold winds, and sometimes also by evaporation (cf. Section 2.1.1), it becomes denser than the water beneath it – this is an unstable situation, so the cooled water tends to sink and displace warmer, less dense water, allowing the mixing to reach to great depths. In certain high-latitude areas, winter cooling is so intense that surface water becomes sufficiently cold and dense to sink down to the sea-bed, contributing to the cold dense waters mentioned in (2) above.

In the temperate mid-latitudes, the winter 'overturn' of water may extend down to 800–1000 m, but the well-mixed layer (often referred to simply as the mixed layer) is generally only several hundred metres thick. This situation is shown schematically on the left-hand side of Figure 4.9 (overleaf). The variation of temperature with depth that results – i.e. the temperature profile – is shown alongside. This has a near-vertical section at the top, corresponding to the mixed layer (where temperature is more or less constant), then a section where temperature decreases relatively sharply with depth. This sloping section corresponds to the *thermocline*, which is the transition zone between the warmer surface waters above and the cold dense water below, where the temperature profile again becomes near-vertical.

Does temperature vary markedly with depth in the deep ocean?

No – the fact that the profile is nearly vertical below 1000 m depth suggests that temperature in the deep ocean is uniformly cold, at 3–4 °C (at least down to 2000 m).

The term thermocline means (vertical) temperature gradient or slope. The thermocline we have just been discussing is often referred to as the *permanent thermocline*, for reasons which will become clear shortly. (In practice, the term is used both for the water in question and the part of the temperature profile that corresponds to it.)

Over the course of spring and summer, the weather becomes calmer, and surface waters gradually warm up. The relatively unstable winter situation, where cold

surface water is easily overturned by wind and waves, is replaced by a very stable situation in which the uppermost layer of water is significantly warmer and less dense. When the ocean is stably 'layered' like this, it is described as *stratified*. In these circumstances, mixing by wind and waves tends to be confined to the uppermost layer, and so the temperature profile acquires a well-defined *seasonal thermocline*, as well as the permanent thermocline below (Figure 4.9).

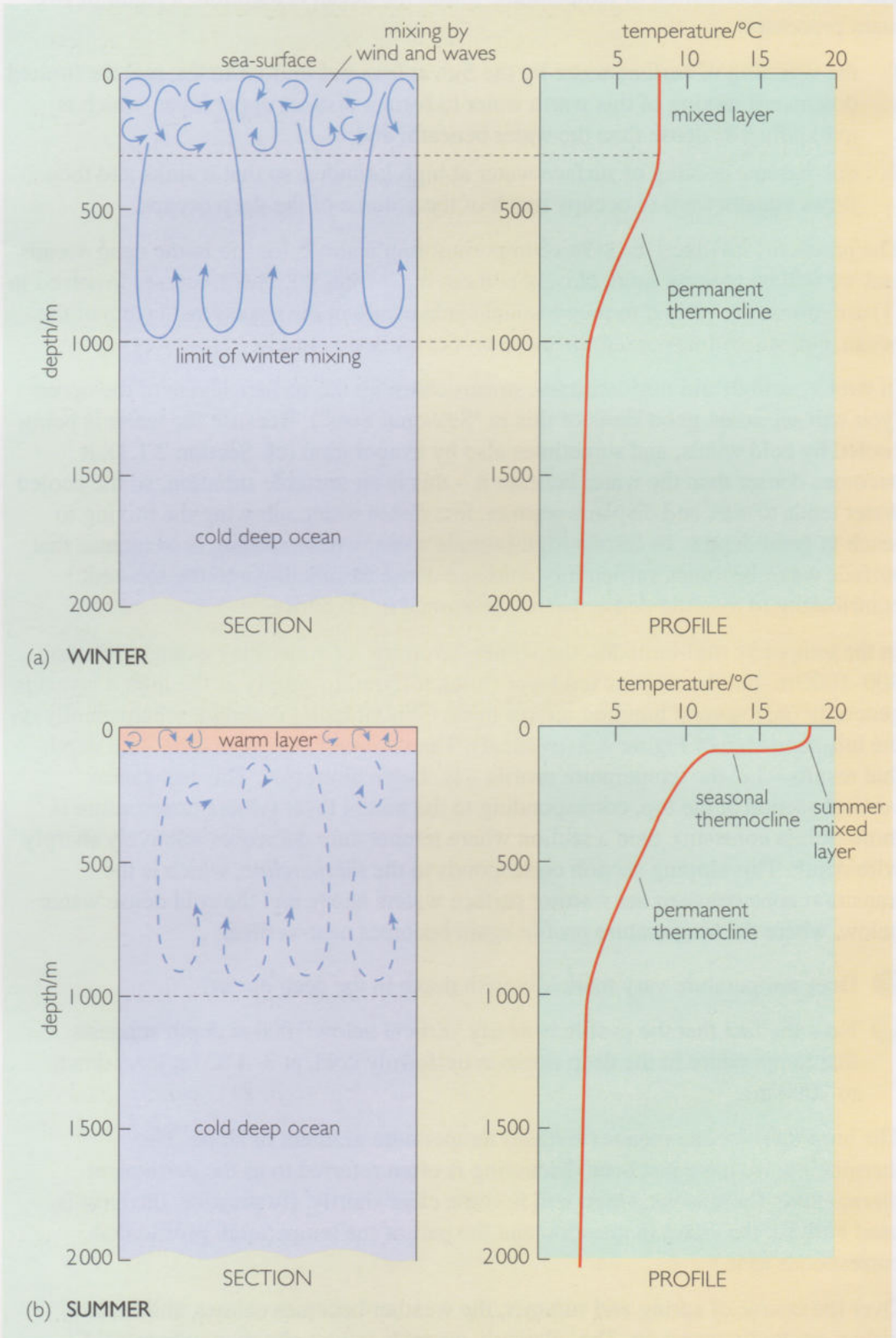


Figure 4.9 Schematic diagrams showing how the vertical distribution of temperature in the oceans in mid-latitudes results from the alternation of winter mixing and summer warming. (a) Cross-section (left) showing winter mixing, and (right) a typical winter temperature profile. (b) Cross-section (left) showing how summer warming produces a thin warm surface mixed layer, and (right) a typical summer temperature profile, with a seasonal thermocline. The effects of winter mixing (dashed arrows) remain, and contribute to the temperature gradient in the permanent thermocline, which is between the well-mixed layer (or seasonal thermocline) and the cold, deep water beneath.

Winter mixing of the surface ocean at high and mid-latitudes is extremely important for life in the oceans, because it mixes up from greater depths dissolved constituents of seawater that are essential for phytoplankton growth, but which have been used up by phytoplankton over the course of the previous summer. These phytoplankton mostly either died or were eaten, and their remains sank down out of the photic zone in small clumps of organic debris known as 'marine snow'. The nutrients that had been taken up by the phytoplankton were therefore removed from the photic zone, and were slowly returned to solution in deeper water during decomposition of the organic material they were part of. You might spot some marine snow in 'Seasonal Seas' – it can be seen clearly in the sequence about lobsters migrating to breed (sequence 8).

As far as phytoplankton are concerned, the most important (non-gaseous) constituents dissolved in seawater are nitrate (NO_3^-), phosphate (PO_4^{3-}) and silica (SiO_2) – these are known as nutrients. Interestingly, these biologically usable forms of nitrogen (N) and phosphorus (P) occur in seawater in the same proportions that they occur in the soft tissues of marine organisms. Nitrate and phosphate are used to make proteins, while silica is used in the external skeletons of certain groups of phytoplankton, notably diatoms.

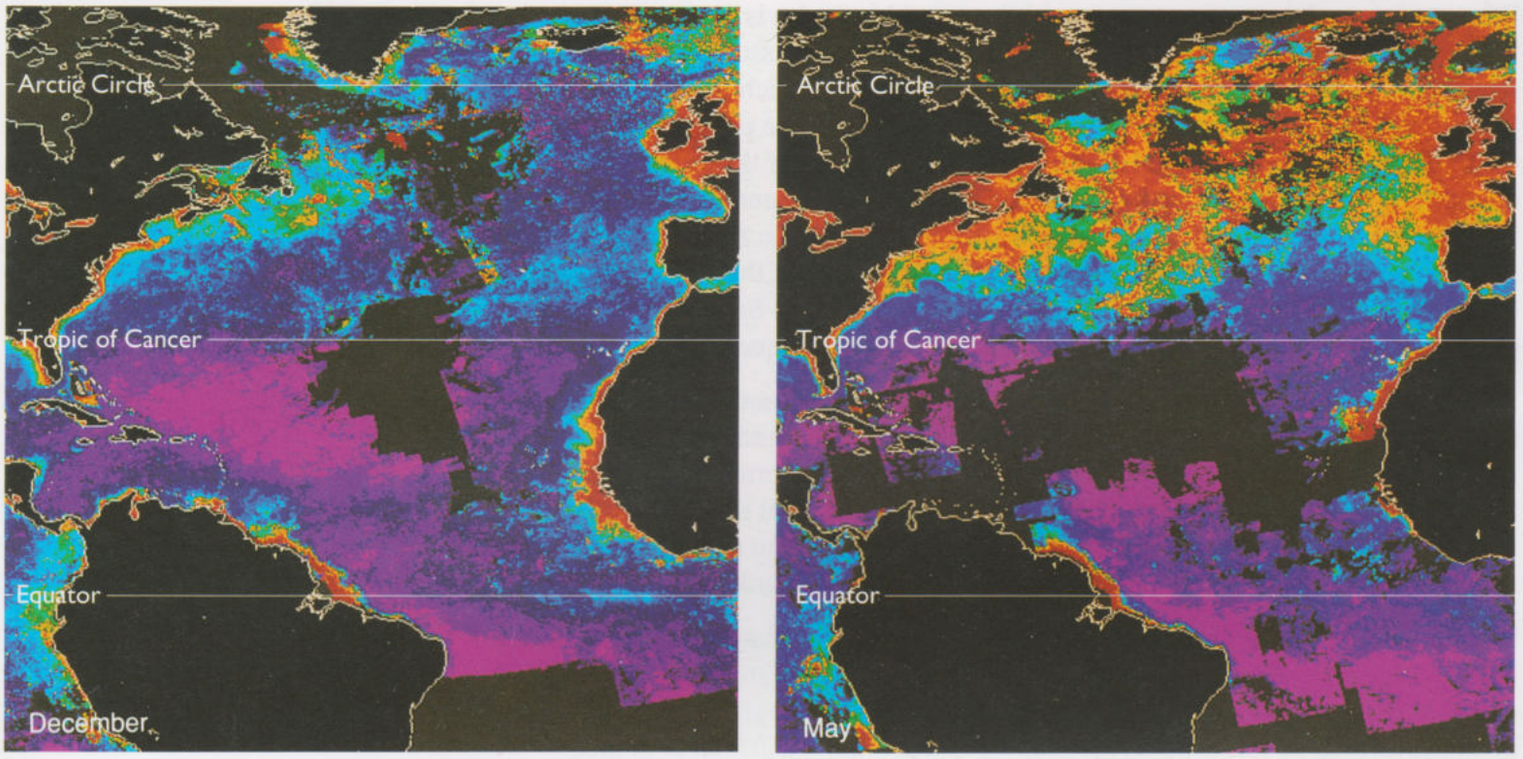
Light levels permitting, it is the concentrations of nutrients that determine how much phytoplankton production can take place. Other constituents are also used – for example, calcium is used to build shells and skeletons, and sodium is one of a number of elements used in soft tissues, but calcium and sodium are available in great abundance in seawater (Table 2.1), so their precise concentrations have no effect on the growth of living organisms. Nitrate, phosphate and silica, on the other hand, may be completely used up by phytoplankton in surface waters, so their concentration may be the limiting factor determining whether or not phytoplankton can continue to grow. In some parts of the ocean, notably much of the Southern Ocean (i.e. around Antarctica) and parts of the Pacific, a shortage of dissolved iron can be a limiting factor. Iron is known as a 'micronutrient' because it is required by phytoplankton in very small amounts.

'Seasonal Seas' is about the spring bloom in temperate waters, including the northern part of the North Atlantic. The satellite images in Figure 4.10 (overleaf) show dramatically the increase in the amount of chlorophyll – i.e. of phytoplankton – in these waters between December and May. The trigger for the spring bloom (as it is often called) is the right combination of sufficiently high light levels, a good supply of nutrients, and a fairly stable upper water column (Figure 4.11, also overleaf).

As described above, in winter, nutrients are brought up from deeper in the ocean by vigorous mixing by wind and waves (Figure 4.11a). However, despite the good nutrient supply, phytoplankton cannot grow because light levels are too low. By early spring, light levels have risen sufficiently for the phytoplankton population to begin to grow, although for individual algae there is still a danger of being carried down into waters where it is too dark to photosynthesise (Figure 4.11b). By late spring the bloom is well underway (Figure 4.11c), and because the seasonal thermocline is beginning to become established (cf. Figure 4.9b) phytoplankton are at less risk of being carried down below the photic zone.

- By referring back to the discussion of Figure 4.9, can you explain why the establishment of the seasonal thermocline tends to keep phytoplankton in the photic zone?

- The formation of a warmer, less dense surface layer results in mixing by wind and waves being mainly confined to that layer.



(a) (b)

Figure 4.10 Seasonal changes in primary production in the North Atlantic, as indicated by the concentration of chlorophyll pigment estimated using the satellite-borne Coastal Zone Color Scanner. Colours are artificial: pink corresponds to lowest concentrations, red to highest concentrations. (a) In December, the only red areas are on the continental shelves and close to coasts, and much of this coloration may be due to large amounts of suspended sediment. (b) By May, the spring bloom is at its peak, and there is high primary production over much of the northern part of the North Atlantic. (Some of the red along coastlines may correspond to high production resulting from nutrients in river run-off, including agricultural fertilisers.)

At the seasonal thermocline, there is a sharp density change between the warmer summer mixed layer and the cooler water beneath. This sharp density change acts as a 'floor' to mixing, and phytoplankton are only carried down below it (and out of the photic zone) during exceptionally rough weather.

By now, the population of zooplankton is also growing and is grazing down the phytoplankton (Figure 4.11c). By mid-summer (Figure 4.11d), not only has a good proportion of the phytoplankton population been eaten, but the nutrient supplies above the seasonal thermocline are significantly depleted.

Figure 4.11 shows the circumstances leading to peaks in phytoplankton and zooplankton numbers in the northern Atlantic, up until mid-summer. In the autumn, there is another bloom of phytoplankton and another peak in zooplankton numbers. Peaks in phytoplankton and zooplankton abundances also occur in other mid- and high latitude waters, but there are important differences from region to region. For example, it seems that in the northern Pacific, phytoplankton abundance is restricted by a shortage of iron, grazing by zooplankton keeps pace with the production of phytoplankton, and the rise in phytoplankton abundance is nowhere near as dramatic as that in the northern Atlantic (Figure 4.10).

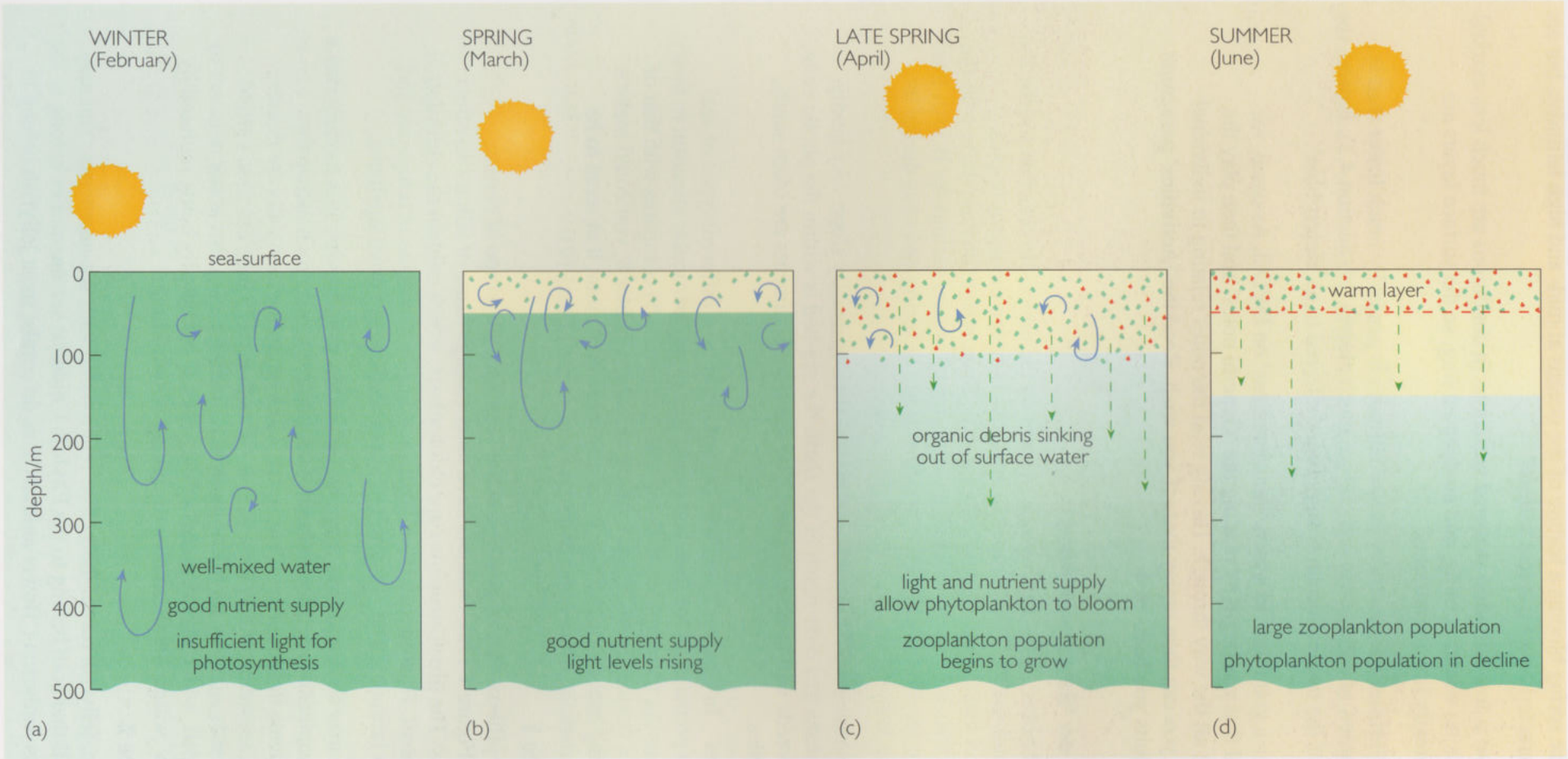


Figure 4.11 Schematic diagrams to show the circumstances that lead up to the spring bloom (a)–(c), and (d) the subsequent depletion of nutrients from surface waters. (a) By February, the water column is well mixed, and surface waters are rich in nutrients (as indicated by the intensity of the green tone). (b) As light levels rise, algae begin to photosynthesise, but tend to be carried down out of the photic zone (shown in yellow) by turbulent mixing. (c) By late spring, phytoplankton are being kept in the photic zone by the existence of the seasonal thermocline. Zooplankton numbers grow, and faecal pellets and remains of dead plankton rain down out of surface waters. (d) By mid-summer, the spring bloom is over, and surface waters have been significantly depleted of nutrients.

Why are spring blooms a feature of the oceans at mid- and high latitudes, but are not characteristic of tropical waters?

Because at low latitudes, seasonal variations in conditions are much less marked. There is no winter cooling, and no deep mixing, so the surface layers are permanently low in nutrients.

As a result, primary productivity at low latitudes is generally much lower than at higher latitudes, and the ocean is therefore much clearer (cf. Section 4.2). Indeed, the clear blue of the tropical ocean is sometimes referred to as 'desert blue'.

▶▶ This is a good time to watch 'Seasonal Seas' on DVD 2. As usual, we recommend that you begin by reading the 'General notes' and then play the programme all the way through. Having read the notes relating to individual sequences, you can then replay them if you wish. Read the 'Activities' paragraph whenever suits you best. ◀◀

Notes on 'Seasonal Seas'

General notes This programme focuses on the temperate seas that overlie the continental shelves. The temperate zone lies between the warm tropics/subtropics and the cold subpolar/polar seas. Such waters include those over the Grand Banks off Newfoundland, and the coastal waters around the British Isles, including the North Sea. The 'story-line' starts in spring and ends during the following winter.

As you know from Chapter 2, continental shelves usually slope very gently, which means that over much of the shelf, the sea-bed is within the photic zone, and seaweeds will be able to grow. The sea-floor sediments are often sandy, with ripples.

Activities In Chapter 8, we will be looking at how different types of seal swim. In preparation for this, you might like to pay particular attention to how the swimming technique of harbour seals (sequence 5) compares with that of sea-otters (sequence 4). Again looking ahead to Chapter 8, you could make a note of any aspects of feeding, or of any other behaviour, that seem to be characteristic of whales and dolphins (sequences 12 and 17).

Sequence 1

- The pillbox-shaped phytoplankton seen here are a type of diatom (cf. Figure 1.11a). Diatoms have outer casings made of silica – in effect, glass. The green structures are chloroplasts, which contain the chlorophyll pigment. Diatoms are often the most conspicuous algae in temperate and high latitudes. The 'swimming' phytoplankton are dinoflagellates.
- You may be wondering why phytoplankton would swim. It is thought that a phytoplankton cell that remained motionless would soon use up the nutrients in the surrounding water. Most phytoplankton cells are denser than seawater, and so tend to sink (though usually they are soon carried upwards again by turbulent motions). Sinking means that water adjacent to the cell, which gets depleted of nutrients, is continually being replaced by 'new' water. An alternative to sinking is swimming!

Sequence 2

- Here, jellyfish reveal their close relationship with sea-anemones. You may recall that both belong to the Phylum Cnidaria; sea-anemones belong to the Class Anthozoa ('flower animals'), as do corals; most jellyfish belong to

the Class Scyphozoa (although the Portuguese man-o'-war, being a siphonophore, belongs to the class Hydrozoa). Not all jellyfish species go through this 'polyp' stage; the floating stage is known as the 'medusa' stage, after the mythical Gorgon with snakey locks.

- Most of the copepods shown here are probably *Calanus finmarchicus*, one of the most abundant planktonic animals of northern temperate and Arctic waters (Figure 1.10c).
- While the copepod is collecting phytoplankton, the narration states: 'On this microscopic scale, water is so viscous that the phytoplankton cannot swim against the current.' This wrongly suggests that the phytoplankton would try to escape! However, the viscosity of the water does help the copepod 'hold on' to algae that it has swept together and assembled between the bristles of its mouthparts; the algae will remain there as long as the mouthparts make only symmetrical movements, because when viscosity is high (as it is for water on the scale of a copepod bristle) symmetrical movements of a fluid just move an object in the fluid back and forth – it doesn't keep going in one direction under its own momentum. (As mentioned in Section 2.1.2, zooplankton themselves are just big enough for the viscosity of water not to prevent them moving forward under their own momentum.)

Sequence 3 Sea squirts (the vase-shaped animals) are chordates, and have tadpole-like larvae. Gorgonians are soft corals. There are also some sea-urchins (echinoderms) here.

Sequence 4

- *Important:* The seasonally high primary productivity off the coast of California is *not* simply the result of the increase in light levels. As you will see in Chapter 5, there is another important trigger here.
- As mentioned in Section 1.3, seaweeds take in nutrients directly from the surrounding seawater. Like phytoplankton, they therefore benefit from the water in contact with their surfaces being constantly renewed, so maximising their supply of nutrients; for this reason, they tend to thrive in turbulent water.
- Note how the blacksmith fish are changing the shapes of their tails. There will be more about tails in Chapter 6.
- Try to make a note of how exactly sea-otters swim, for comparison with the harbour seals later.
- Bryozoans are sometimes called 'moss animals'. In the majority of species, each tiny individual (< 0.5 mm across) is largely encased in an external skeleton of calcium carbonate. As shown here, they feed by capturing small planktonic organisms or particles of organic debris, using a special food-trapping device which consists of numerous tentacles with cilia (hairs). There are almost 4000 marine species of bryozoans (a few living at depths of more than 8000 m) but their ecological significance has not really been investigated.

Sequence 5

- As mentioned in connection with 'Tidal Seas', seagrasses are flowering plants, not algae. Eelgrass (*Zostera marina*) is very widespread in shallow waters around the Atlantic, eastern Pacific and Mediterranean.

- How does the harbour seal's swimming technique compare with that of the sea-otter? (Don't spend a lot of time on this.)

Sequence 6

- Rays are related to sharks (as you will see in Chapter 6). Try to observe the bat ray's swimming technique.
- Note the red and brown coloration of many of the seaweeds, and the sandy nature of the sea-floor. The parallel ripples indicate a gentle current.

Sequence 7 Sea-slugs are molluscs with no shell or a greatly reduced one. Most species are carnivorous, and live near the shore (there are a few species which swim in the water column, e.g. *Melibe*, coming later (sequence 14)).

Sequence 8

- Note the marine snow drifting down.
- The seaweed being eaten by the baby crab is sea lettuce (*Ulva*), mentioned in Section 3.2.2.

Sequence 9 Note the octopus's eyes: they are well developed and their overall arrangement is rather similar to those of vertebrates. It may surprise you to know that octopi (along with squid and cuttlefish) are molluscs.

Sequence 10

- mentioned earlier, mysid shrimps are crustaceans belonging to the sub-class Peracarida. Peracarids typically have a carapace that projects forward over their heads. They are most common in estuaries and inshore waters (some are harvested commercially in parts of Asia). However, they are not generally abundant in the planktonic community, and many species spend much of their life on the sea-floor or in deeper water.
- Sharks and dogfish (sequence 13) are closely related. We will be saying more about them in Chapter 6.

Sequence 11 The phytoplankton have mostly 'disappeared' partly because they have been eaten by zooplankton and other animals, and also because the levels of sunlight are now so low that very little photosynthesis can occur. However, a few individuals do survive to form the basis of next year's 'crop'. Also, some types of phytoplankton, including diatoms and dinoflagellates, have dormant stages, known as resting spores. These spores, which have tough shells, sink to the bottom until favourable conditions return.

Sequence 14 The particles in the water column are bits of organic debris, probably mostly from the dying kelp itself.

Sequence 15

- The phytoplankton that you can see here (including chains of diatoms) are superimposed artificially – as you know, they are microscopically small.
- Note how the squid are propelling themselves along.

Sequence 16 Can you see how the sea dragon is propelling itself along?

Sequence 17 Swimbladders will be discussed in Chapter 6.

4.4 Meroplankton – just passing through

The term meroplankton means 'temporary plankton' and it refers to planktonic stages of animals, both nektonic and benthic, that spend only part of their life cycle as a member of the plankton. (Plants and animals that spend their entire lives floating in the water column are classified as holoplankton.) Meroplankton are most abundant in shelf seas, where about 70% of the larger benthic invertebrates (i.e. those more than 1 mm across) release eggs or embryos into the water column. Depending on the species, these meroplankton may spend a few minutes to several months (or even years, in exceptional cases) as part of the plankton.

As you saw in 'Seasonal Seas', planktonic young come in an amazing variety of shapes, mostly very different from the adult forms (Figure 4.12, overleaf). Benthic snails and clams produce tiny shelled young, which have a distinctive membrane edged with tiny hairs (cilia), used for 'swimming' and collecting food (Figure 4.12a, b). Many benthic organisms produce planktonic larvae that go through a number of stages, sometimes separated by moulting. Some animals, including crabs and lobsters, have a final planktonic stage that resembles the adult – this is known as a 'megalopa'; a crab megalopa can be seen in 'Seasonal Seas' (sequence 8) and in Figure 4.12j.

Although some fish species lay their eggs on or within the sea-bed sediment, or attach them to seaweed, many – including tuna, sardines and anchovy – produce free-floating eggs. Fish eggs and fish larvae form an important part of the meroplankton. In a single spawning, one female may produce several hundred thousand eggs. As you will see in 'Open Ocean', the eggs are tiny transparent spheres, usually only 1–2 mm in diameter. They carry a supply of transparent yolk, and in some cases also a globule of oil, presumably to help keep them buoyant. (We return to the reproductive strategies of different groups of fish in Chapter 6.)

4.5 The oxygen minimum layer

As discussed in Section 2.1, surface waters have a high concentration of dissolved oxygen, partly because oxygen is produced as a by-product of photosynthesis (Equations 1.1a and 4.1), and partly because waves churn bubbles down into surface waters.

What biological processes remove oxygen from solution?

Respiration by plants (mainly phytoplankton) and by animals, and decomposition.

Bacterial decomposition of organic matter sinking out of the photic zone (dead organisms, faecal pellets and other organic debris) – i.e. bacterial respiration – means that at some depth below the surface, the concentration of dissolved oxygen begins to decrease. The organic debris tends to sink more slowly through the permanent thermocline because the marked temperature decrease is accompanied by a marked *density increase*. The slowly sinking organic debris attracts large numbers of zooplankton, and the decomposition, combined with respiration by the zooplankton (and other animals feeding on them), means that oxygen concentrations decline to a minimum, usually somewhere between 400 and 800 m depth. Below this oxygen minimum layer, the concentration of dissolved oxygen begins to increase again, because the cold deep water which originally sank from the surface at high latitudes carries large amounts of oxygen.

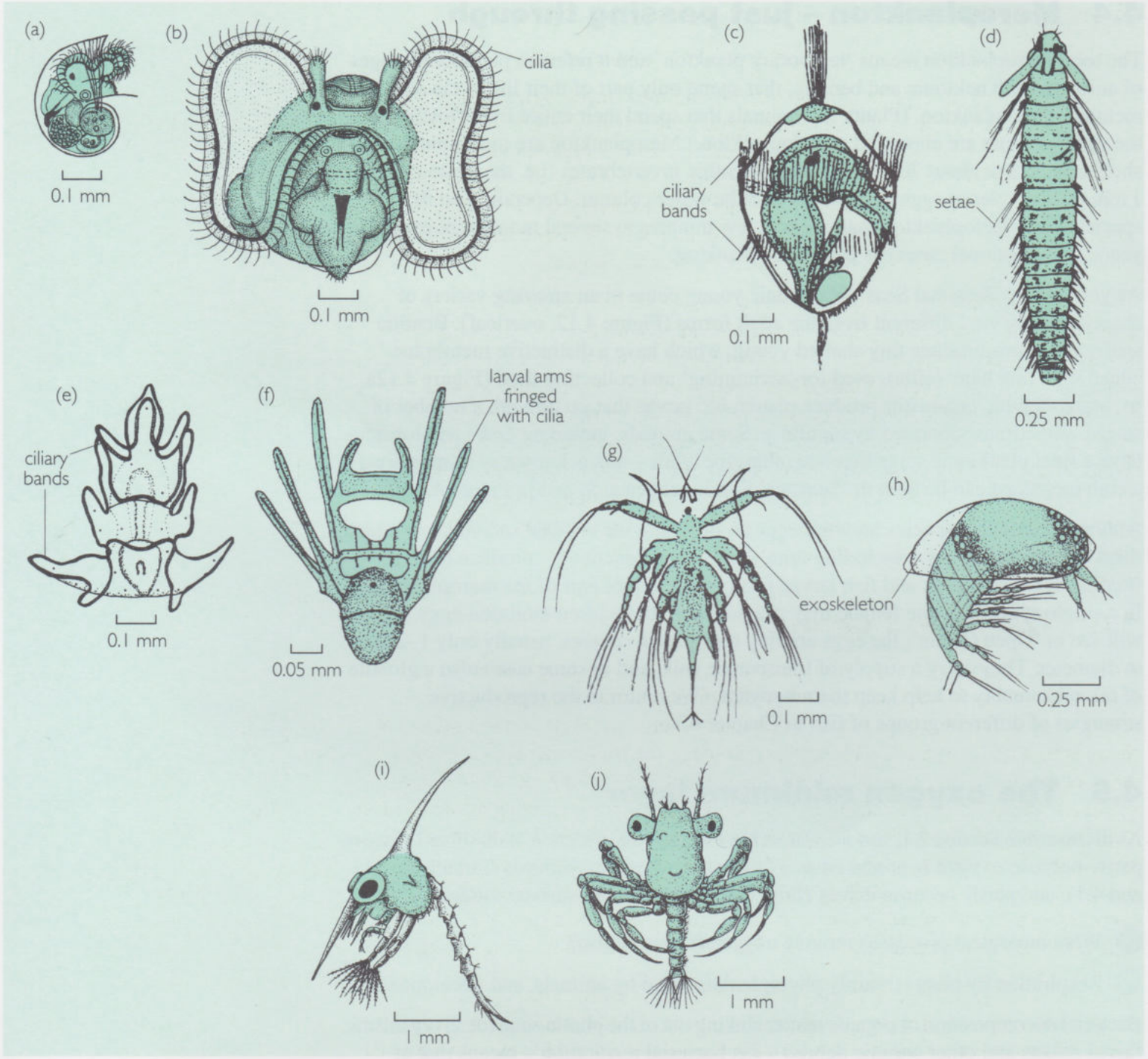


Figure 4.12 A selection of meroplanktonic larvae of benthic invertebrates at various stages of development (not all drawn to the same scale). (a) Larva of the gastropod mollusc *Nassarius reticulata* just after hatching; (b) late larva of the same species, with a spiral shell forming (just visible, lower left). The 'wings' are typical of planktonic gastropod larvae, and are edged with cilia or hairs used for both swimming and feeding (also visible on the larvae in c, e and f). (c) Early larvae of a polychaete worm and (d) late larvae of a polychaete worm with the characteristic bristles already visible. Both (e) and (f) are echinoderms, a starfish and a sea-urchin, respectively. (g) Barnacle larva and (h) late barnacle larva, which will settle on a hard surface and metamorphose into the adult form. (i) Spiny 'zoea' larval stage and (j) final 'megalopa' larval stage of the crab *Portunus puber*.

Thinking back to Section 2.1, can you suggest why this might be?

Cold water can hold more dissolved gas than can warm water.

The degree of oxygen depletion in the oxygen minimum layer varies from place to place, depending largely on the amount of organic debris falling from surface waters. The greatest depletion tends to occur where the 'oceanic' oxygen minimum layer impinges on the continental shelf or slope, where large amounts of organic debris could be accumulating beneath highly productive coastal waters. This situation is found in the northern Arabian Sea and in association with the Benguela Current off south-west Africa (for reasons that will become clear in Chapter 5).

At depths where there are marked oxygen minima, the biomass of pelagic animals is reduced, and relatively few species can survive in conditions with very little dissolved oxygen. If oxygen-depleted water upwells to the surface, it can cause mass mortalities of fish and invertebrates. However, low oxygen concentrations do not necessarily mean a shortage of animals – for example, enormous populations of spider crabs have been observed feeding on the organic-rich sediment on the continental margin off Oman, in the lower part of the oxygen minimum layer. In the open ocean, certain species – e.g. the grotesque 'vampire squid' (*Vampyrotheuthis infernalis*) – have become adapted to live permanently within the low-oxygen layer, while other animals migrate in and out of it.

4.6 The sound channel

We mentioned in Section 2.1.1 that sound can travel long distances in the ocean without much loss in intensity. In fact, it can travel 1000 km or more – let's look briefly at how this can happen. Imagine a sound source (a whale, say), sending out sound waves in the ocean (cf. Figure 2.2). Some of the sound energy is absorbed by the seawater itself, and some is scattered as a result of bouncing off bubbles and suspended particles. The intensity of the sound also declines with increasing distance from the whale, as the sound energy spreads out over a wider and wider front, in all directions. However, for reasons that we do not need to go into, sound waves produced at a depth where the speed of sound is at a minimum will remain at that depth, spreading out sideways, but with relatively little spreading up and down. This is therefore the optimum depth for long-distance communication in the ocean.

Question 4.4 The speed of sound in the ocean increases with increasing temperature and with increasing pressure (and is only slightly affected by salinity). Given this information, and the temperature profile in Figure 4.9a, explain why there is a minimum in the speed of sound at around 1000 m depth. Begin by discussing how the speed of sound changes with depth in the thermocline, given the extra information that temperature generally has a greater effect on the velocity of sound than pressure. ◀

This minimum in the speed of sound is known as the sound channel. It is not always at exactly the same depth, but it always corresponds roughly with the bottom of the permanent thermocline. Its existence is certainly known about by whales, which use it for communication over distances of 1000 km or more.

We have seen that winds are important for life in the oceans because they generate waves, which mix up the surface layers of the ocean and affect the distribution of nutrients, the supply of dissolved oxygen, the vertical temperature distribution and

the stability of the water column. Waves also beat upon the coasts and shoreline, and locally contribute to the patterns of zonation of intertidal organisms. On a global scale, winds are important because they drive the surface currents, which – as you will see in the next chapter – have far-reaching effects on life in the ocean.

Winds, currents and life

5

In the introductory programme, we are told that 'currents, more than any other factor … control the distribution of nutrients and life around the globe'. You will now appreciate that mixing by wind, and the establishment of a seasonal thermocline, play an important role in promoting high productivity in temperate waters. Wind also plays a crucial role in driving currents, not only surface currents but also, in certain locations, *vertical* movements of water.

In Sections 5.2 to 5.4, we will look at how wind and current patterns lead to low concentrations of nutrients in the surface waters of the open oceans, as well as at various causes of locally high nutrient concentrations and high biological productivity.

5.1 The global wind system

The uneven heating of the Earth by the Sun gives rise to the global wind system, the large-scale pattern of air movement within the atmosphere which – along with surface currents – redistributes heat from low to high latitudes. Figure 5.1 (overleaf) shows the prevailing winds over the Earth's surface in July and January, along with the mean patterns of high and low atmospheric pressure. These are *average* pictures – on any one day in July or January the wind and pressure pattern could look completely different from either of the patterns shown here. Another important result of averaging is that small-scale features are 'smoothed out', so Figure 5.1 shows only relatively large-scale features of the global wind pattern.

The most persistent winds are the Trade Winds, which can be seen on Figure 5.1 mainly between the Tropic of Cancer and the Tropic of Capricorn, and blow generally westwards and towards the Equator. Winds are named for the direction they blow *from*, so these winds are known as the North-East Trade Winds and the South-East Trade Winds (sometimes 'Trades' for short).

The purple line is the Intertropical Convergence Zone (ITCZ), which is the zone of low pressure where the wind systems of the two hemispheres meet, and where air carried in the Trade Winds rises, before eventually beginning to move poleward. Winds blow from regions of high pressure to regions of low pressure, so if the Earth were not spinning, the Trade Winds would blow directly southwards and northwards (from the high pressures of the subtropics, shown red/pink in Figure 5.1), towards the ITCZ. It is because the Earth is spinning towards the *east* that the air in the Trade Winds moves *westwards* in relation to the Earth (i.e. not simply towards the ITCZ) – you can think of this as the air being 'left behind' by the Earth turning beneath it. Away from the Equator, the fact that the Earth is rotating *combined* with the fact that it is spherical, results in moving air in the Northern Hemisphere tending to be deflected to the right relative to the Earth, and moving air in the Southern Hemisphere tending to be deflected to the left relative to the Earth. This phenomenon is known as the *Coriolis effect*; it influences both winds and currents and, perhaps surprisingly, it indirectly has a profound effect on life in the oceans.

Study the arrows around the regions of high and low pressure in Figure 5.1.

In which direction, clockwise or anticlockwise, do winds blow around areas of high pressure (1) in the Northern Hemisphere, (2) in the Southern Hemisphere?

(1) Winds blow clockwise around areas of high pressure in the Northern Hemisphere, and (2) anticlockwise around areas of high pressure in the Southern Hemisphere.

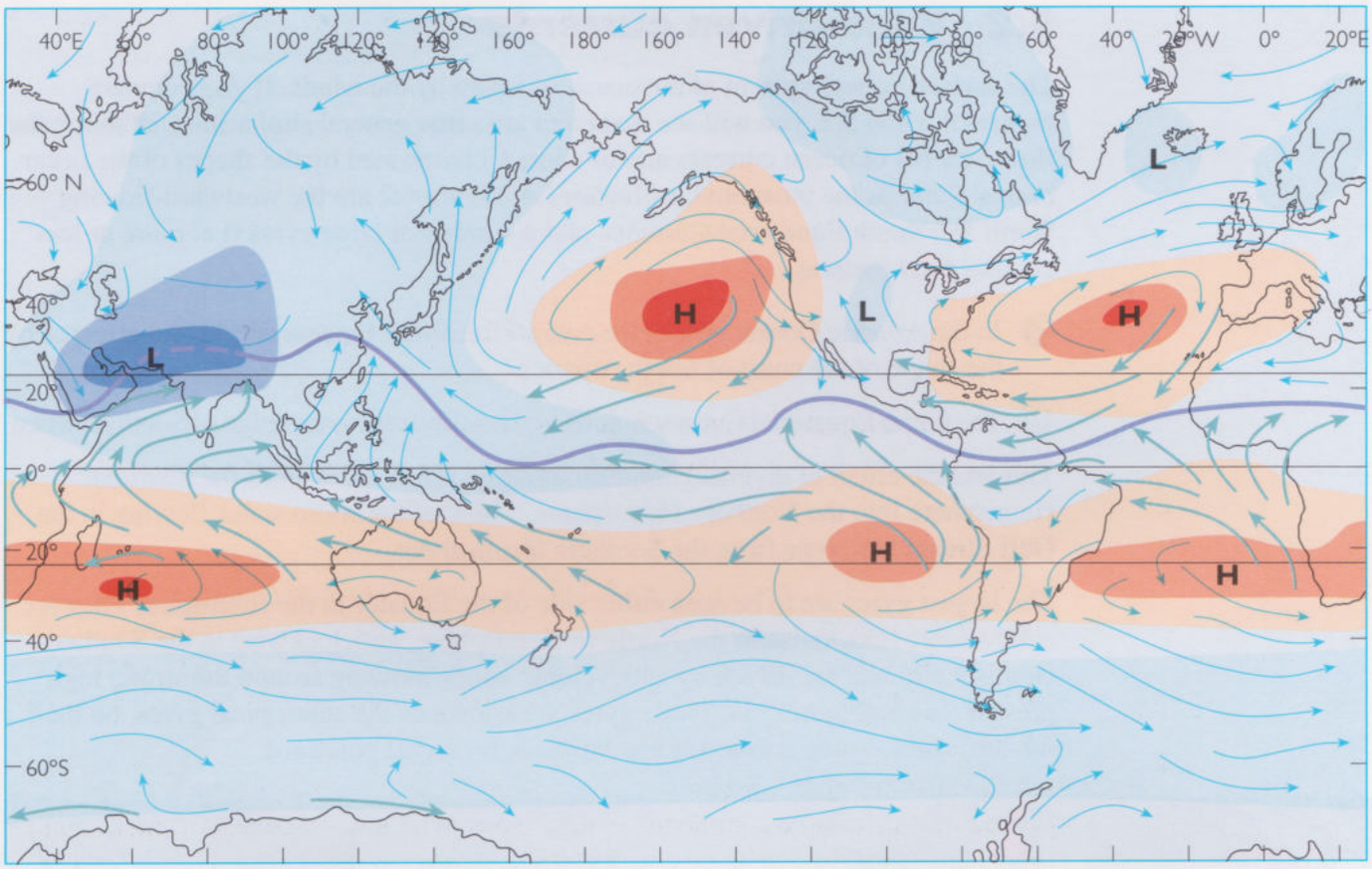
Figure 5.1 (*opposite*) The prevailing winds at the Earth's surface, and the position of the Intertropical Convergence Zone (ITCZ) where the wind systems of the two hemispheres meet, in (a) July (northern summer/southern winter) and (b) January (southern summer/northern winter). Also shown are the positions of the main regions of high atmospheric pressure (red/pink tones) in the subtropics, and low atmospheric pressure (blue tones) at low latitudes and in subpolar regions, at those seasons of the year. Note the positions of the Tropics of Cancer and Capricorn (23.4° N and 23.4° S).

- In which direction do winds blow around areas of low pressure? (This is easiest to see in Figure 5.1b.)
- Winds blow anticlockwise around areas of low pressure in the Northern Hemisphere (and clockwise around areas of low pressure in the Southern Hemisphere).

Whichever hemisphere they are in, winds that blow around *high* pressure areas are referred to as *anticyclonic*, and winds that blow around *low* pressure areas are referred to as *cyclonic*. So, if you were watching a storm warning on a TV weather forecast for Australia, the winds around the low pressure centre would be clockwise; whereas in the Northern Hemisphere, we see low pressure centres with anticlockwise winds.

If you compare Figures 5.1a and 5.1b you will see that in summer, atmospheric pressure over the large continental masses tends to be low, whereas in winter it tends to be high. Over the ocean, by contrast, the general positions of the regions of high and low pressure remain in more or less the same place over the course of the year (although their relative strengths vary significantly). This indirectly affects the salinity of surface waters, because while high pressure is associated with dry, settled weather and generally clear skies, low pressure centres – whether tropical cyclones, or the lows (depressions) typical of temperate latitudes – are associated with moist air, clouds and rain. The Intertropical Convergence Zone, for example, gives rise to very heavy precipitation, and this lowers the salinity of surface waters in equatorial latitudes. Being of relatively low salinity, as well as very warm, the uppermost layer of water at extremely low latitudes is markedly less dense than the water below. This gives rise to a strongly stratified water column – i.e. one that is highly stable and not easily mixed – so the surface waters tend not to be replenished with nutrients from below. Thus, the high rainfall at low latitudes indirectly contributes to the 'barren' nature of the waters there (cf. end of Section 4.3).

By contrast, surface waters under the clear skies of the subtropical highs lose much more freshwater by evaporation than they gain from rainfall, and so they have relatively high salinity. In 'Tidal Seas' (sequence 18), you saw flamingos and brine shrimps living in the highly saline coastal shallows around the Bahamas. These islands lie just to the south-east of Florida, and so the waters around them are subjected to quite high evaporation, especially under the influence of the North-East Trades (Figure 5.1). The exceptionally high salinity of the waters around the islands is the result of the fact that they are the highest part of a large shallow region known as the Bahama Bank. Because the waters are so shallow, they warm up quickly and are subject to high rates of evaporation; furthermore, the high salinity waters that result tend not to be diluted by less saline waters from adjacent areas.



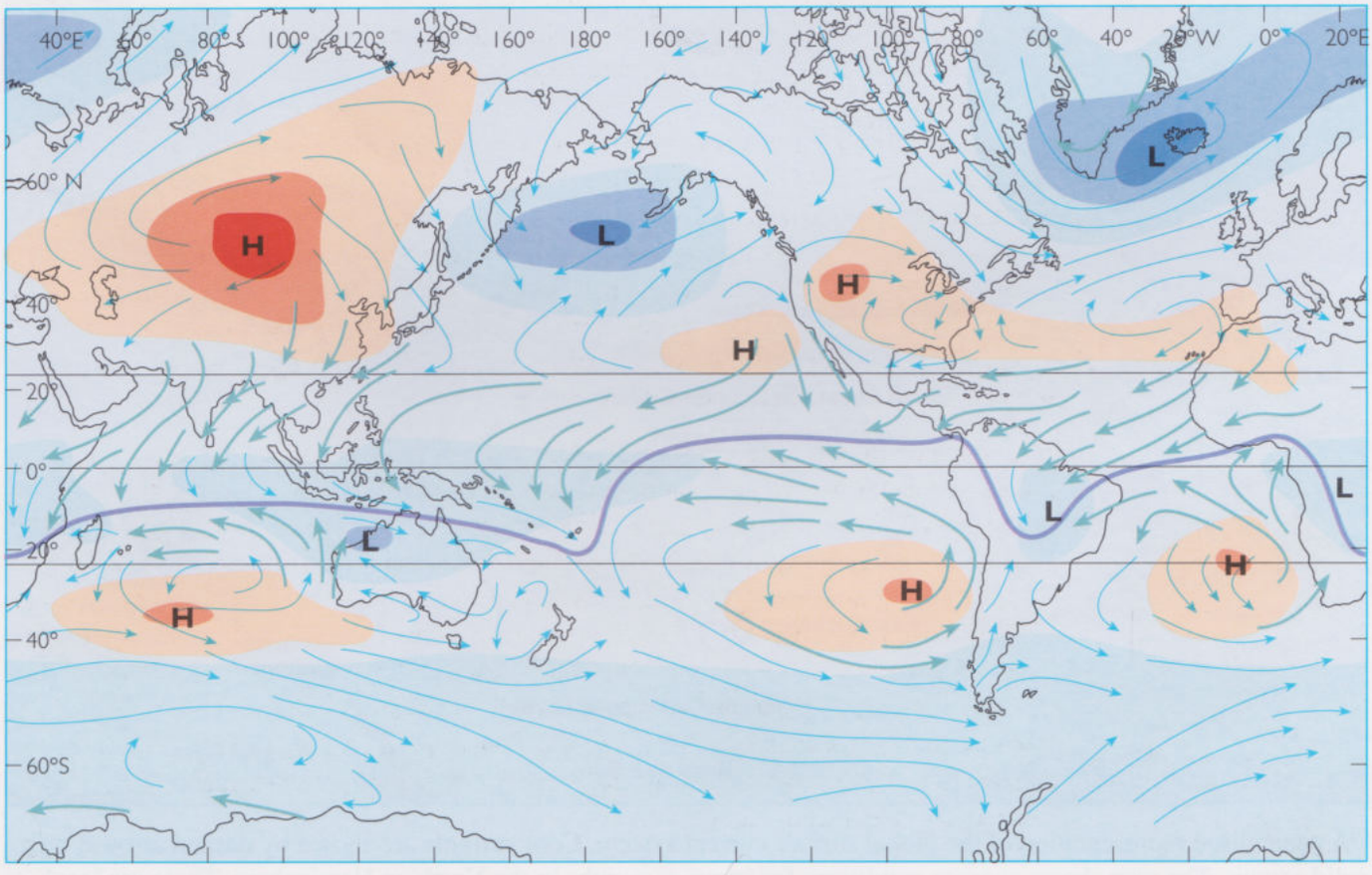
(a) JULY

KEY

mean position of ITCZ

most frequent wind direction

prevailing wind direction (≥50% of observations)



(b) JANUARY

5.2 Wind-driven currents

The surface current system of the ocean is driven by the winds. If you compare Figures 5.1 and 5.2, you will see that there are some general similarities, although the flow patterns of ocean currents are, of course, constrained by the shapes of the ocean basins. Perhaps the most obvious features of Figure 5.2 are the westward-flowing North and South Equatorial Currents, and a number of large gyres (i.e. more or less circular flow patterns).

In the Atlantic Ocean, how is the path of the South Equatorial Current affected by the shape of the coast of South America?

The South Equatorial Current is deflected northwards by the bulge of South America.

This has the effect of diverting large amounts of warm water from the Southern Hemisphere into the Northern Hemisphere. Much of the warm water flowing in the Gulf Stream has come from the Southern Hemisphere.

The largest gyres are to be seen either side of the Equator in the subtropics. They are anticyclonic (clockwise in the Northern Hemisphere, anticlockwise in the Southern Hemisphere) and are driven by anticyclonic winds blowing around the strong high pressure areas (Figure 5.1). These gyres are known as the subtropical gyres; on their western sides, water warmed at low latitudes is carried poleward.

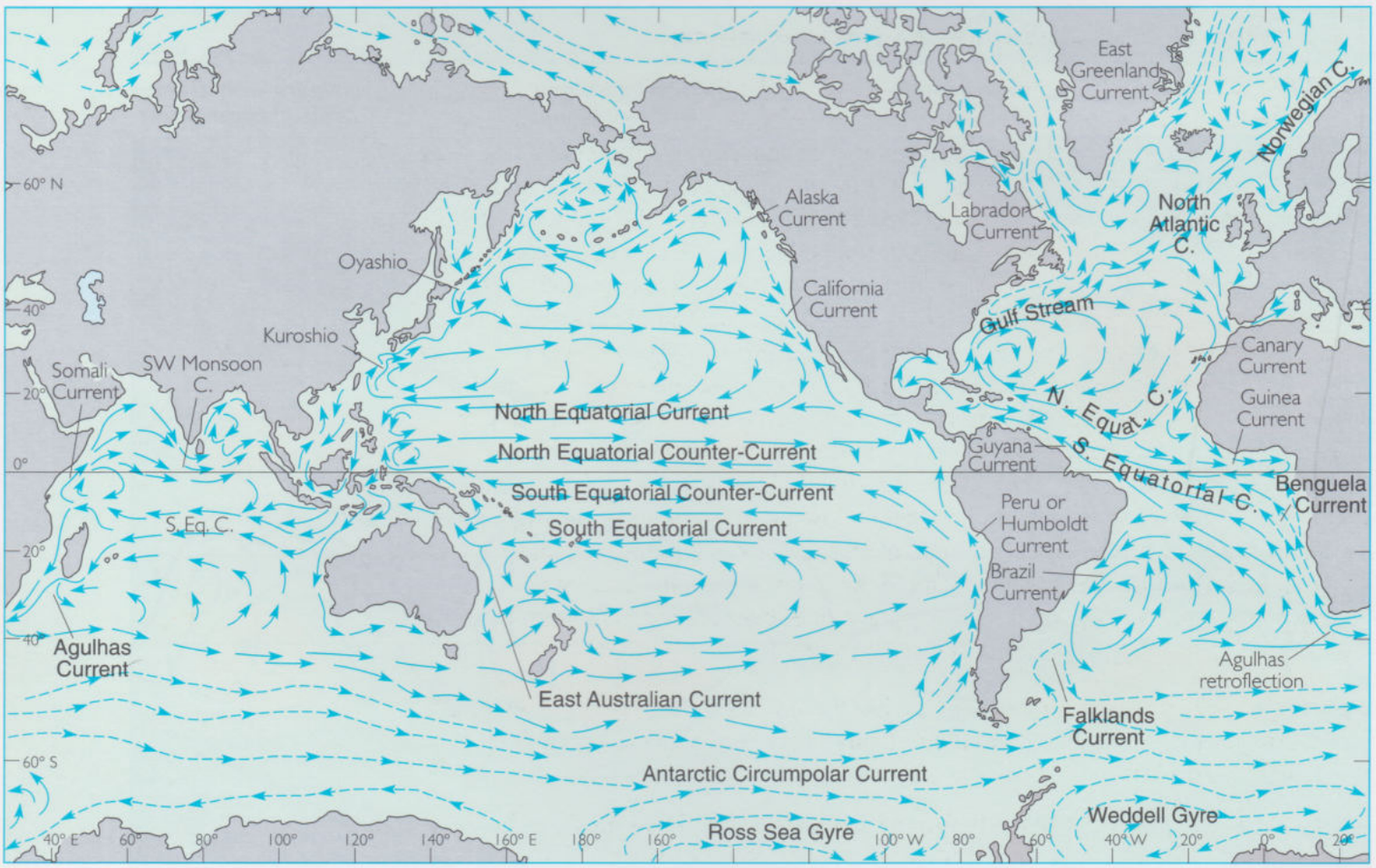


Figure 5.2 A generalised representation of the global surface current system. Cool currents are shown by dashed arrows; warm currents by solid arrows. The map shows average conditions for summer months in the Northern Hemisphere. There are local differences in the winter, especially in regions affected by monsoons (seasonally reversing winds).

Question 5.1 Which poleward-flowing currents carry warm water from equatorial and tropical regions in (1) the North Atlantic and North Pacific, (2) the South Atlantic, and (3) the southern Indian Ocean? ◀

As suggested by the arrows in Figure 5.2, the poleward-flowing currents you have identified are fast and intense (arrows close together), in contrast to the equatorward-flowing currents on the opposite sides of the oceans, which are slow, wide and diffuse (arrows far apart). The former are often referred to as 'western boundary currents', and the latter as 'eastern boundary currents'. Eastern boundary currents are, of course, cold or cool, because they are carrying water from high latitudes, i.e. from polar and subpolar regions.

Identify the eastern boundary currents in (1) the North Atlantic and North Pacific, and (2) the South Atlantic and South Pacific.

They are (1) the Canary Current and the California Current, and (2) the Benguela Current and the Peru or Humboldt Current.

In tropical and subtropical regions, the redistribution of heat by the surface current system means that, at a given latitude, water temperatures on the western side of the ocean are typically higher than those on the eastern side of the ocean. This is the reason (alluded to in Section 2.1.2) why temperature-related distributions of species are not quite in zones parallel to the Equator.

5.2.1 Wind-driven upwelling and downwelling

As discussed above, eastern boundary currents are colder than western boundary currents because they flow from high latitudes, whereas western boundary currents flow from low latitudes. However, eastern boundary currents are also cold for another reason. Because of the Coriolis effect, away from the Equator, surface water moving in response to a persistent wind does not flow exactly parallel to the wind, but at an angle to it – to the right of the wind direction in the Northern Hemisphere and to the left of the wind direction in the Southern Hemisphere. The uppermost layer of sea being 'dragged along' by the wind in turn drags the layer of water below it, and that in turn drags the one below, and so on, down to the depth where the effect of the wind is no longer felt (the thickness of the wind-driven layer varies between a few tens of metres and 200–300 m, depending on the time of year). Now, the slower a wind or current is moving, the greater the deflection caused by the Coriolis effect, so the direction of motion of each layer is deflected slightly more than that of the one above. The overall effect is that, if the wind has been blowing for some time, the *average* motion of the wind-driven layer is at right angles to the wind, to the right of the wind direction in the Northern Hemisphere and to the left of the wind direction in the Southern Hemisphere. This can have dramatic consequences for primary productivity (i.e. the rate of primary production) in coastal waters.

Imagine a stretch of coastal seas in the Northern Hemisphere. What do you think will happen if a persistent wind blows along the coast, in such a way that the coast is on the left?

The layer of surface water under the influence of the wind will move to the right (as this is in the Northern Hemisphere), i.e. it will move offshore.

A comparable situation will arise if a persistent wind blows along a Southern Hemisphere coast in such a way that the coast is on the right. In both cases, the surface water moving offshore allows deeper, more nutrient-rich water to rise to take

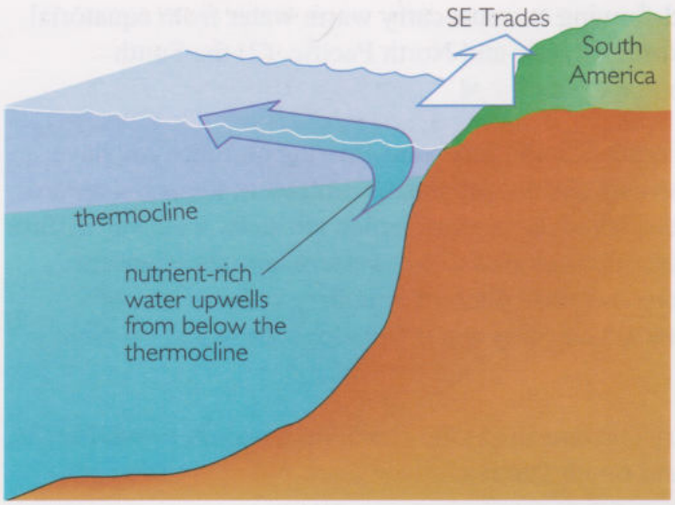


Figure 5.3 Schematic diagram to show how equatorward winds along eastern coastlines give rise to upwelling of nutrient-rich water. Here, the South-East Trade Winds blowing along the coast of Peru and Ecuador give rise to motion of the wind-driven layer offshore. As this is in the Southern Hemisphere, the wind-driven layer moves to the *left* of the wind direction.

its place. Once in the photic zone, this nutrient-rich water will support high levels of phytoplankton growth, and hence also large populations of zooplankton and of animals further up the food chain. (*Note*: this nutrient-rich water upwells from 100–200 m depth at most; it does *not* upwell from great depths as is commonly supposed.)

Some of the most biologically productive coastal upwelling regions are found in the tropics and subtropics on the eastern sides of the oceans where, at certain times of year, the Trade Winds blow along the coast (Figure 5.1). The best known such upwelling region is probably that off the coast of Ecuador and Peru (Figure 5.3). It is this upwelling that fails when the South-East Trades weaken during the climatic fluctuations known as El Niño events. Another rich upwelling region is that within the Benguela Current, off south-west Africa (Figure 5.4).

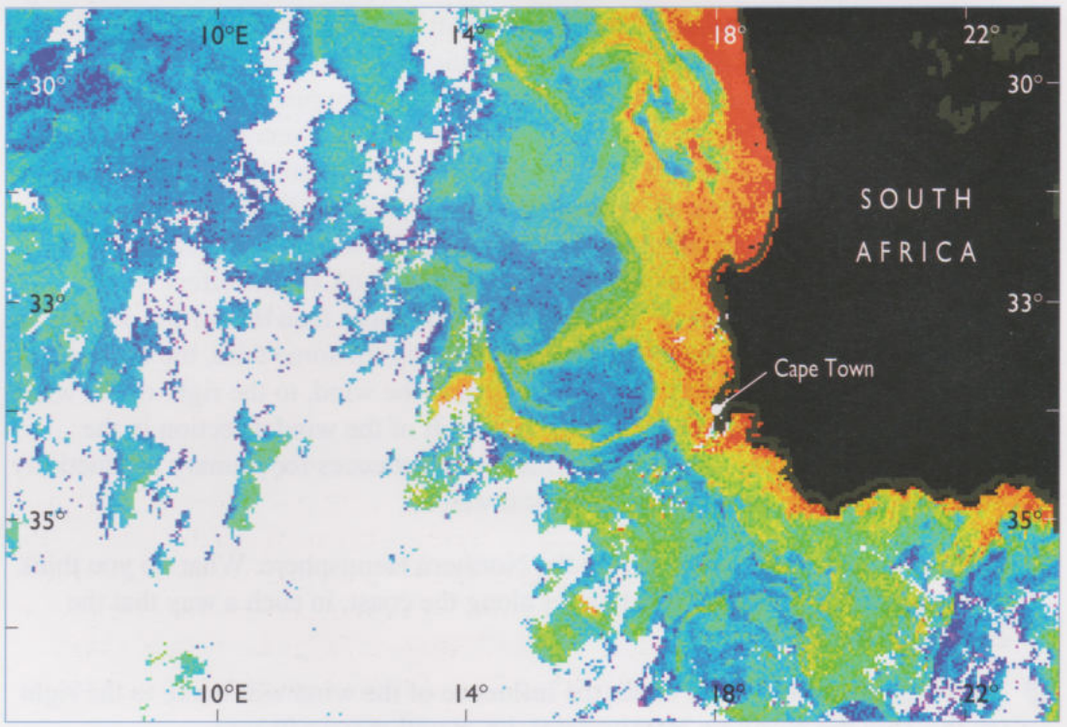


Figure 5.4 Coastal Zone Color Scanner satellite image showing the southernmost end of the zone of upwelling and high productivity which occurs off the coast of south-west Africa, in the Benguela Current. Colours are artificial: red corresponds to high concentrations of chlorophyll pigment, pale blue to very low concentrations (white is cloud). Note how complicated the flow patterns are, with wave-like features and filaments of productive water streaming out into the open ocean.

The dramatic seasonal growth of the kelp forests off the coast of California, seen in 'Seasonal Seas' (sequence 4), is partly a result of the increased intensity of solar radiation in spring and summer, as suggested by the narration. However, the reason for the exceptionally high productivity is nutrient-rich water supplied from below by upwelling. This occurs all year round off southern California, and peaks in late spring and early summer off northern California (cf. the wind directions in relation to the coast in Figure 5.1).

'Bounty off Natal' (which you can watch shortly) shows huge 'slicks' of sardines. The narration suggests that the sardines are there because nutrient-rich water has flowed into the region as a result of reversal of the Agulhas Current – which is the western boundary current (the equivalent of the Gulf Stream) in the southern Indian Ocean (cf. Figure 5.2). In fact, the Agulhas Current does *not* reverse, but at certain times of year it moves away from the Natal coast, allowing colder, more nutrient-rich water, which usually flows northwards at depth along the continental shelf, to come to the surface. Along the coast, therefore, warm southward-flowing water is replaced by cold, northward-flowing water. It is not known for sure why this situation arises – it may be related to the wind pattern, or perhaps to the effect of eddies ('swirls' or vortices) in the Agulhas Current.

▶▶ You can watch 'Bounty off Natal' on DVD 2 now, if convenient, or save it until later (it lasts about 8 minutes). ◀◀

Notes on 'Bounty off Natal'

General note As usual, make a note of any behaviour which seems to be characteristic of whales and dolphins.

Sequence 2

- Gannets are amongst the deepest-diving of those seabirds that catch their prey by plunging into the sea (as opposed to pursuing it underwater as penguins and cormorants do).
- The whale which arrives at the end of the 'feasting' is also known as Bryde's whale. It is a baleen whale, and a rorqual, so is a member of the same taxonomic family as the blue whale (Figure 1.8). Species of rorquals can be distinguished from one another by their size, colour, the number of throat grooves (this species has 47–70), and the number of baleen plates (this species has 250–370). Rorquals live mainly on plankton, and will eat fish only if they are in large schools, as here. Note the way the throat bulges when the whale feeds.

Upwelling of nutrient-rich water also occurs in mid-ocean, away from coasts, again as a result of surface water moving apart, or *diverging*, in response to wind patterns. In the eastern Atlantic and the eastern Pacific, there are extensive bands of upwelling just to the south of the Equator, and parallel to it; these arise because the South-East Trade Winds cross the Equator, leading to a moving apart of surface waters known as the Equatorial Divergence (Figure 5.5 overleaf). Ringing the globe in the Southern Ocean is another zone of wind-driven divergence of surface water, which also leads to high productivity. This is known as the Antarctic Divergence.

The effects of the Antarctic Divergence and the Equatorial Divergence can both be seen to some extent in the distribution of primary production shown in Figure 4.1. Other areas of high production can be seen in the northern North Atlantic and the

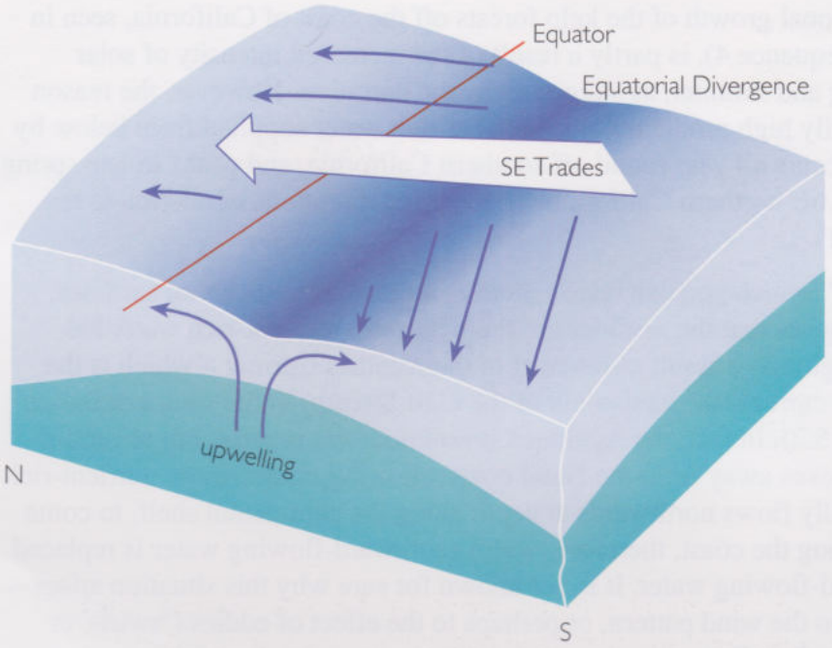


Figure 5.5 Schematic diagram showing why upwelling occurs at the Equatorial Divergence. The South-East Trade Winds blow across the Equator. Because of the Coriolis effect, the wind-driven layer to the south of the Equator moves to the left, at right angles to the wind. However, in the vicinity of the Equator itself there is *no* Coriolis effect, and the wind-driven layer moves in the *same* direction as the wind. As a result, there is a zone parallel to the Equator where surface waters are driven apart, allowing deeper, more nutrient-rich water to rise up into the photic zone. This is the Equatorial Divergence.

northern North Pacific – the areas affected by the spring plankton blooms discussed in 'Seasonal Seas'.

According to Figure 4.1, which regions have the lowest primary productivity of all? According to Figures 5.1 and 5.2, what wind and current patterns characterise these areas?

The areas with the lowest primary productivity are the central parts of the subtropical gyres, which are driven by the anticyclonic wind systems blowing around the subtropical highs.

Figure 5.6a shows why the central parts of the subtropical gyres have such low productivity. The diagram illustrates the situation in the Northern Hemisphere, where anticyclonic winds are clockwise and the Coriolis effect causes deflection to the right of the wind direction. The result is the same in the Southern Hemisphere, where anticyclonic winds are anticlockwise and the Coriolis effect causes deflection to the left of the wind direction. In summary, in a subtropical gyre the average motion of the wind-driven layer is towards the centre of the gyre. Water converges and 'piles up' in the centre of the gyre and gradually sinks. As a result, the sea-surface is dome-shaped, with the centre of the gyre being nearly a metre higher than the outer parts. The bottom of the mixed layer and the thermocline (Section 4.3) are correspondingly deeper in the middle of the gyre and shallower towards the edge.

A deep thermocline, and a thick mixed surface layer within which water is generally sinking, is not conducive to deeper, more nutrient-rich water being mixed up into the photic zone. This is why the central parts of the subtropical gyres have such low primary productivity. Furthermore, phytoplankton in a thick mixed layer are always at risk of being carried down out of the photic zone by mixing. If this happens, they will not be able to absorb enough light to grow and reproduce, and may even die as a result.

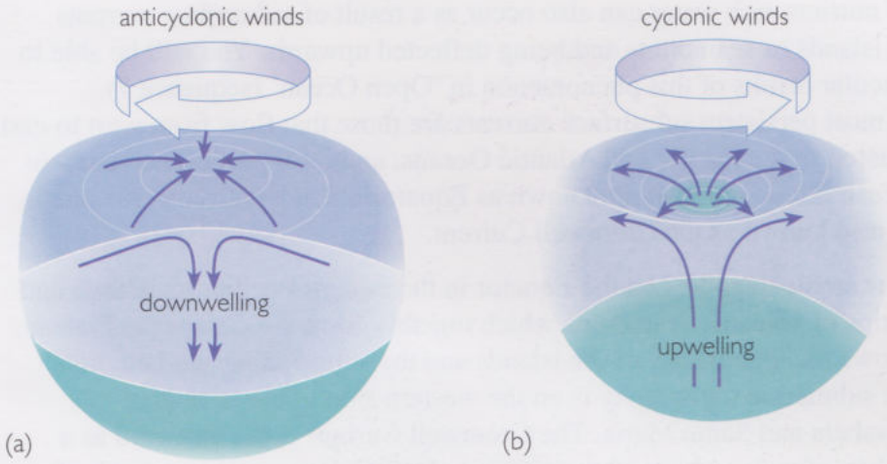


Figure 5.6 Schematic diagrams showing (a) how anticyclonic winds lead to convergence of surface water and downwelling, while (b) cyclonic winds lead to divergence of surface water and upwelling. Although the thermocline is in reality a depth *zone*, here it is shown simply as the boundary between the surface layer (pale blue) and deeper, more nutrient-rich water (turquoise). (Both diagrams are drawn for the Northern Hemisphere.)

The clear waters of the subtropical gyres are the setting for 'Open Ocean'. These waters are clear because there are such small populations of phytoplankton and zooplankton. As you will see shortly, open ocean ecosystems function very differently from those of productive upwelling areas.

Earlier, we noted that the high productivity of the spring bloom in the northern temperate seas shows up clearly on Figure 4.1. In Section 4.3, we discussed how the timing of the spring bloom is affected by light levels and the extent to which the upper water column is stratified or well mixed. However, to appreciate fully how the northern parts of the Atlantic and the Pacific come to have such high levels of productivity, we need also to remember their oceanographic setting.

Look again at Figure 5.2. Generally speaking, how would you describe the surface current patterns in the northern North Pacific and the northern North Atlantic?

In both areas, surface currents are flowing anticlockwise – in other words, the currents are forming *cyclonic* gyres. (In the northern Pacific, there seem to be two such gyres, linked together.)

Just as deflection of wind-driven currents by the Coriolis effect causes surface water to move towards the centres of anticyclonic gyres, so it also leads to surface water moving *away from* the centres of cyclonic gyres (Figure 5.6b). As a result, the centres of cyclonic gyres – including the subpolar gyres we have just been discussing – are regions where surface waters diverge, the thermocline comes closer to the surface, and deep nutrient-rich water tends to upwell to the surface (especially in winter, when winds are strongest). This helps to ensure that surface waters within cyclonic gyres are 'restocked' with high concentrations of nutrients every winter.

5.3 The effects of islands

Islands and seamounts disrupt current patterns, and may support oases of high productivity in otherwise barren waters. One way in which this occurs is known as the 'island wake effect': surface currents flowing around islands form eddies, and as a result there is vigorous vertical mixing on the downstream side of the islands. Satellite images often show plumes of highly productive water swirling downstream from islands.

Upwelling of nutrient-rich water can also occur as a result of *subsurface* currents encountering islands or seamounts and being deflected upwards. You will be able to see the spectacular results of this phenomenon in 'Open Ocean' (sequence 7). Amongst the most persistent subsurface currents are those that flow from west to east along the Equator, in the Pacific and Atlantic Oceans, and – for part of the year – in the Indian Ocean. These currents are known as Equatorial Undercurrents; the one in the Pacific is also known as the Cromwell Current.

The Galápagos archipelago lies on the Equator in the eastern Pacific. Its islands and islets are the tips of volcanic seamounts which together form the Galápagos Plateau. Figure 5.7 shows the topography of the islands and the surrounding sea-bed: note how steep the submarine topography is on the western side of the islands of Fernandina, Isabela and Santa Maria. The Cromwell Current flows eastward as a horizontal ribbon of water which, in the vicinity of the Galápagos is at a depth of about 100 m. On reaching the steep submarine slopes of the Galápagos Plateau, it splits into filaments (blue arrows on Figure 5.7) and is deflected upwards, coming to the surface in some places.

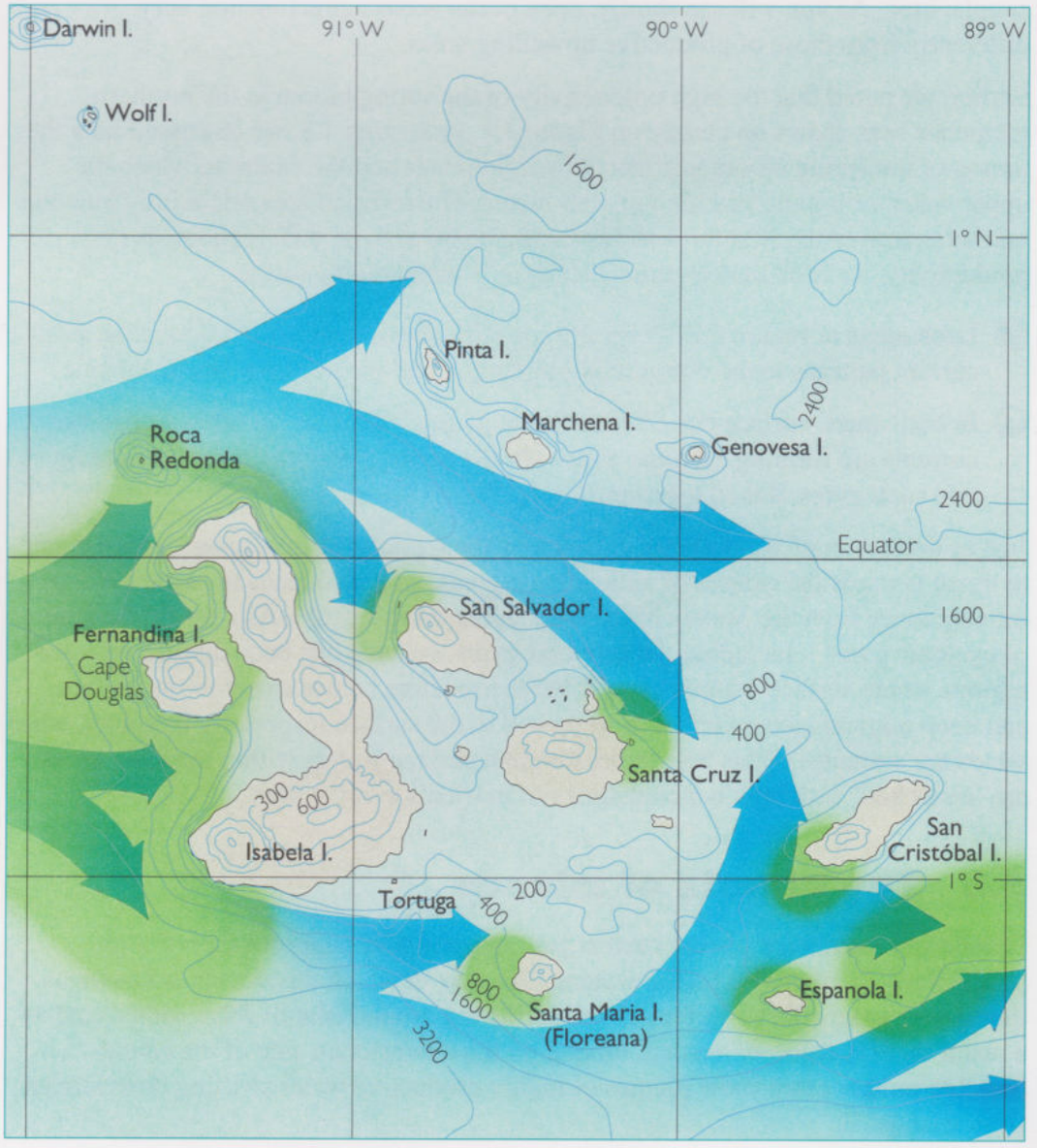


Figure 5.7 The most common flow paths of the Cromwell Current (Equatorial Undercurrent) through the Galápagos archipelago (blue arrows), and the locations of the most persistent upwellings (green areas). The contour depths in the ocean, and heights on land, are given in metres. Note how close together the contours are – i.e. how steep the submarine topography is – on the western side of the islands of Fernandina, Isabela and Santa Maria.

Cape Douglas, home of the marine iguanas seen near the beginning of the introductory programme, is on the north-western tip of Fernandina (see Figures 5.7 and 5.8).

Question 5.2 By reference to Figures 5.7 and 5.8, explain why Cape Douglas is a good site for marine iguanas to live. ◀

Perhaps surprisingly, animals like fur seals and penguins, which usually only live at high latitudes, are *also* found on the western side of the Galápagos archipelago. This is partly because the upwelling Cromwell Current water is significantly colder than the surrounding surface water. Another reason is that the Galápagos islands lie at the edge of the zone of equatorial upwelling discussed earlier – the Equatorial Divergence. Furthermore, they lie in the path of the South Equatorial Current (Figure 5.2) – this is cold not only because it comes from the Southern Ocean but also because it carries cold water upwelled along the coast of South America (cf. Figure 5.3). Galápagos penguins now form a distinct species endemic to the islands (i.e. found only there). Being a Southern Hemisphere cold-water group, they would have reached the Galápagos via the coast of South America, in the cold waters of the Peru Current.

Figure 5.8 Summary map of observed and inferred distribution patterns of coral reef communities and seaweed (macrophytic) communities around the islands of the Galápagos archipelago.

5.4 Fronts

Towards the beginning of 'Open Ocean', the narration refers to 'vast current systems, like immense rivers' and states that 'the boundaries between these masses of moving water form invisible barriers that can trap both plankton and nutrients carried up from the depths'. However, it is important to appreciate that ocean currents are *not* like rivers – maps like Figure 5.2 represent *average* conditions. If you were to measure the surface current somewhere in the region labelled 'Gulf Stream' on Figure 5.2, you might well find that at that moment the current direction at the point in question was quite different from the direction suggested by the arrows in Figure 5.2, perhaps even in the opposite direction. Even powerful, relatively well-defined currents continually shift and change their positions to greater or lesser extents, forming meanders and loops, or splitting into filaments.

5.4.1 Frontal currents and 'rings'

Western boundary currents like the Gulf Stream and the Kuroshio are particularly prone to forming meanders and loops like those in Figure 5.9. Such currents are sometimes known as 'frontal currents' because they flow along the boundaries – fronts – between different bodies of water, often referred to as 'water masses'. This terminology arises by analogy with that used in meteorology, where fronts are the boundaries between different air masses. Fronts in the ocean are the 'invisible barriers' referred to in the narration.

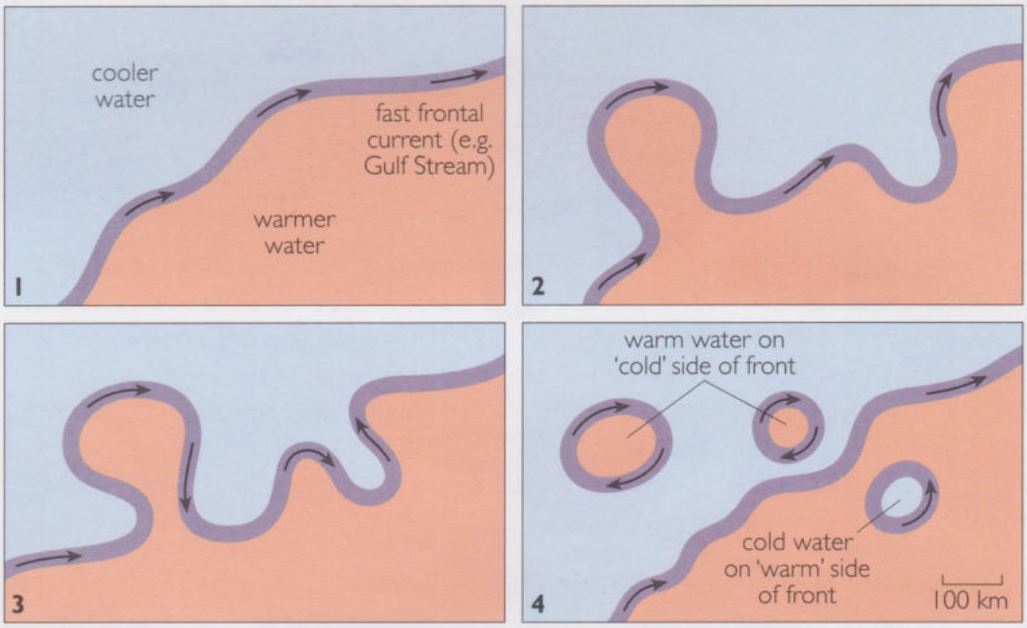


Figure 5.9 Plan-view diagram showing how meanders in strong frontal currents like the Gulf Stream can develop into 'rings'. The formation of such rings results in water on one side of the current being transferred to the other.

For reasons we do not need to go into here, it is the difference in density between two adjacent water masses – that is, the density gradient across the boundary zone – that determines the speed of the frontal current which flows along the boundary zone. The Gulf Stream flows along the boundary zone between cold coastal water (which is further cooled by the cold waters of the Labrador Current; cf. Figure 5.2), and the warm water of the Sargasso Sea (the central part of the subtropical gyre, to the east of the Gulf Stream). Gulf Stream water itself is warm, having flowed from low latitudes via the Gulf of Mexico.

Figure 5.10 is a 'false colour' satellite image of the waters off the coast of eastern North America and Canada, showing concentrations of chlorophyll pigment. The

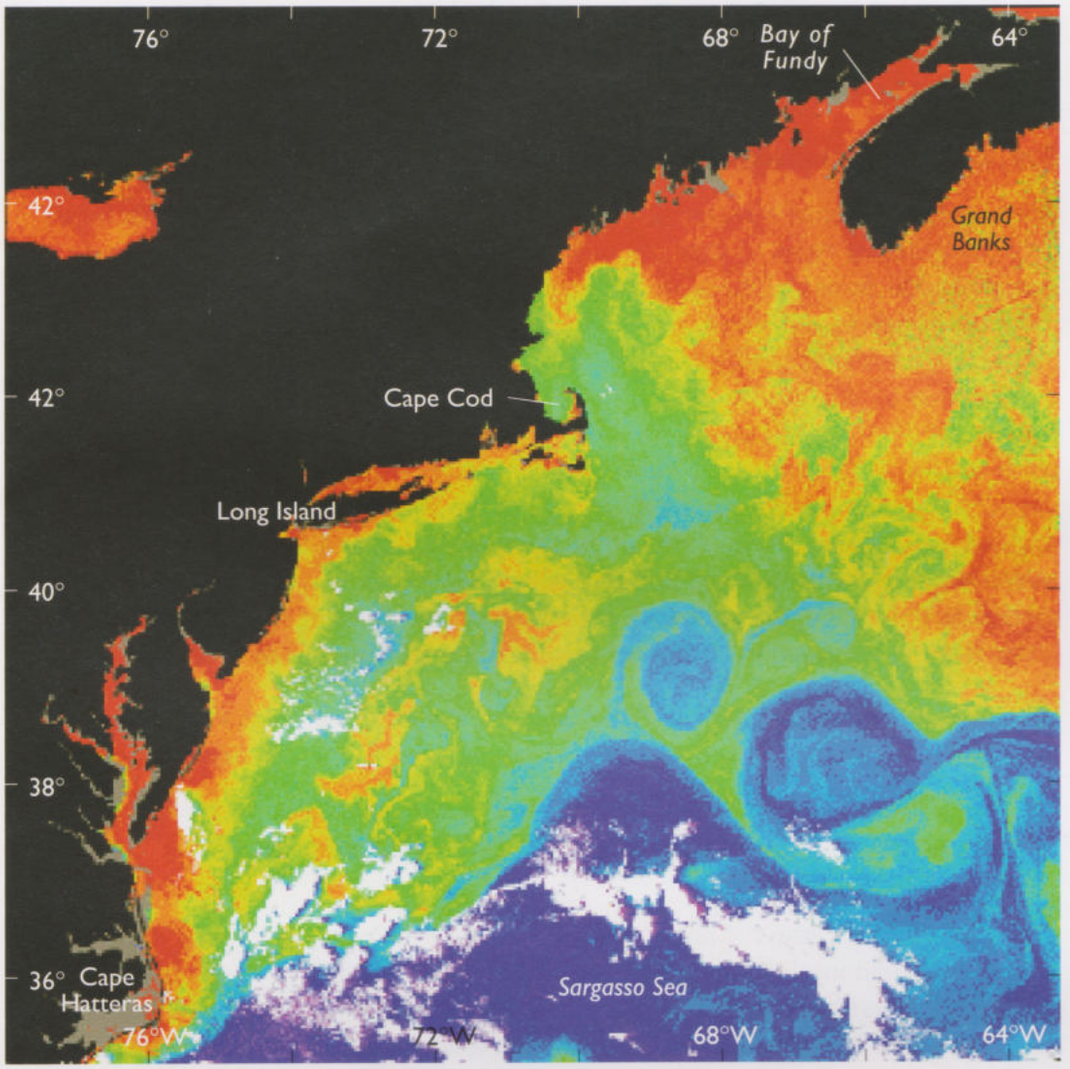


Figure 5.10 Coastal Zone Color Scanner satellite image of the waters off the north-eastern seaboard of the United States and Canada. Colours are artificial: red corresponds to the most productive water (i.e. that with the highest concentrations of chlorophyll pigment), blue to the least productive water (white is cloud). The red area to the top right is the productive water overlying the Grand Banks, until the early 1990s the site of a major commercial cod fishery. You can also see the Bay of Fundy, whose productive waters were the subject of part of 'Tidal Seas'.

warm and unproductive waters of the Gulf Stream and the Sargasso Sea can be seen to the lower right (in blue), while the cool productive coastal water can be seen to the west and north of this (in green, yellow and red). We would like you to focus on the blue feature shaped like an upside-down comma, to the north of the Gulf Stream, near the centre of the image. This is a Gulf Stream ring, a meander of the Gulf Stream which has 'pinched off' and become isolated (cf. Figure 5.9). To the right of this, you can see a meander which had not yet pinched off at the time this image was recorded, but probably did so shortly afterwards.

In which direction is the water in the ring in Figure 5.10 rotating?

It is rotating clockwise (i.e. anticyclonically) – you can tell this because of the way it formed from the Gulf Stream, which is flowing (roughly) from west to east (i.e. from left to right).

Rings like these are being continually generated to either side of all strong frontal currents. Biologically, they are important because their formation results in a column of water from one side of the current being transferred to the other side. In this case, a column of warmer, less nutrient-rich water, containing organisms typical of the Sargasso Sea, has formed from a clockwise meander of the Gulf Stream and then been left spinning in the cold, nutrient-rich waters to the north of the Gulf Stream (which have their own organisms). Similarly, columns of nutrient-rich water may be transferred to the Sargasso Sea side of the Gulf Stream by the formation of an

anticlockwise meander. It is not known what the long-term ecological significance of these transfers of water might be, but it *is* known that the rings themselves can persist for months or even years.

5.4.2 Fronts related to sea-bed topography

There are a number of reasons why high productivity can be associated with fronts between different types of water. Sometimes the sea-bed topography plays a role in generating the front and the high productivity. In Chapter 3, we discussed the productive well-mixed water of continental shelves and shelf seas. The boundaries between this well-mixed water and deeper, stratified and less productive waters are often known as *tidal mixing fronts*. Figure 3.4 shows how the water over the continental shelf around the British Isles is more productive than deeper water to the north and west. There is also a clear boundary (front) between the extremely well-mixed water in the shallower, southern part of the North Sea (where the colour of suspended sediment obscures that of the phytoplankton) and the deeper, less well-mixed water in the central and northern part of the North Sea. (As mentioned in the caption to Figure 3.4, the yellowish coloration off the coast of Norway, where the water is deep, is caused by dissolved organic material flowing out from the Baltic.)

Looking back to Figure 3.4 and its caption, would you say that there is any evidence for increased productivity along the *edge* of the continental shelf?

Yes, there are blooms of coccolithophores (white areas) along the edge of the continental shelf off Scotland and Ireland (as well as over the continental shelf itself, in some places).

There are various causes of high productivity along the edges of continental shelves. Sometimes, tidal mixing stirs up so much sediment that primary productivity over the shelf itself is restricted by lack of light. In these cases, the highest production tends to occur along the boundaries between well-mixed water and stratified water, i.e. along the fronts. At the very edge of the continental shelf (cf. Figure 2.7), there may be *shelf break fronts*, where deeper nutrient-rich water moves up the continental slope into a more stable, shallower part of the water column, giving rise to high primary productivity. This occurs along the edge of the continental shelf off Nova Scotia, and also along the coast of Natal (seen in 'Bounty off Natal').

Locally, there are often fronts off river mouths, around the edge of the outflowing plume of river water. Being fresher and less dense, the river water flows above the seawater, and tends to entrain deeper water into it. This could be more nutrient-rich than the river water and, if light levels are sufficiently high, could give rise to high primary productivity. Of course, the situation varies from river to river, and the position of the phytoplankton bloom is affected by the strength of the outflow and by local currents. As suspended sediment greatly affects the amount of light available for photosynthesis, the position of the bloom is also affected by how much sediment the river carries and how long it takes to settle out. Of course, river outflows themselves often lead directly to high primary productivity, especially if they carry nitrates leached from fertilised land, or phosphates from sewage effluent.

▶▶ This is a good time to watch 'Open Ocean' on DVD 2, which looks at life in the clear waters of the nutrient-poor subtropical gyres, and at the isolated 'oases of life' found within them. However, if you have not already watched 'Bounty off Natal', you should look at that first. ◀◀

Notes on 'Open Ocean'

General note During this programme, we see tuna at different stages in its life cycle – egg, tuna larva, young tuna and adult – and in different parts of its circuit of migration. There will be more about fish migrations in Chapter 9.

Activity While watching, make a note of any features that seem to be characteristic of fast-swimming species like tuna. Pay particular attention to their body shapes and the shapes of their tails.

Sequence 1 Note how streamlined the Sei whale is while swimming, and not feeding. Note also the water streaming from the whale's jaws, as the sardines are sieved out.

Sequence 3

- Fish eggs form part of the meroplankton. The round object is a globule of oil to help the egg float.
- In Chapter 9, and part II of 'The Deep', you will discover more about these nightly migrations up from the depths. The latest theories about how bioluminescence evolved will be discussed in Chapter 10.
- You will now be well aware that currents are not like rivers, and that these 'invisible boundaries' are fronts!

Sequence 4

- As you know from Sections 2.1.1 and 4.6, sound travels through water with very little loss of energy, so dolphins can detect disturbance in the water some distance away and use their echo-location to track down the cause. Echo-location involves pinpointing the position of a target by bouncing sound off it. A stream of discrete sounds is emitted and a 'fix' is made using the time taken for the sound to travel to the target, bounce off it, and travel back again.
- The blue-fin tuna's 'special blood vessels' (which all tuna have to some extent) will be discussed in the next chapter.

Sequence 5 The coil of jelly is a chain of *salps* (Phylum Chordata). Individual salps have cylindrical gelatinous bodies with an opening either end. Each salp spends part of its life cycle as an individual, and produces a chain by 'budding' to form identical copies of itself. Depending on the species, individual salps may be 1–30 cm long, and chains (which may consist of several hundred individuals) may be as long as 15 m. Salps live mainly in warm surface or near-surface waters and feed on phytoplankton and bacteria.

Sequence 6

- Triggerfish are so-called because their forward dorsal fin (i.e. the fin along the back which is closest to the head) consists primarily of a single rigid spine that normally lies against the fish's body, but which can be extended as a weapon if the need arises.
- The significance of 'bony fish' will become clear in Chapter 6.

Sequence 7

- This volcano is probably erupting over a 'hot spot' (cf. Section 2.2).
- During this sequence, you can see the results of upwelling generated by steep submarine topography, like that which occurs to the west of the western Galápagos islands (cf. Figure 5.7).
- Characteristic features of sharks will be discussed in the next chapter.

- Note that the anchoveta are warned of the approaching predators because they feel the vibrations that the predators generate as they swim. You may remember from Section 2.1.2 that this is possible underwater because (unlike air) water is almost incompressible. You will learn more about how fish detect water movements (including those generated by sound waves) in Chapter 6.
- As you will now appreciate, currents shift all the time, in response to fluctuations in the wind or as a result of interactions with other currents. If the current that is being forced up by the seamount moves to one side of it, the upwelling will cease.

Sequence 8 The Azores are steep-sided volcanic islands, so upwelling will be generated off them.

5.5 Ecosystems and food webs

'Open Ocean' covers both the nutrient-poor waters of the subtropical gyres and some isolated upwelling regions. As you will see shortly, open ocean ecosystems function very differently from the ecosystems of productive upwelling areas like those to the west of the Galápagos archipelago, or coastal upwelling regions in eastern boundary currents such as the California Current and Benguela Current (Figure 5.4).

5.5.1 Food chains and food webs

A food chain is a linear representation of the feeding interactions in an ecosystem or community of organisms, in which each organism (or group of organisms) is food for the next member in the sequence; each link in the food chain represents a transfer of organic matter and hence energy. Figure 5.11 shows three representative food chains for three types of marine waters. Food chain (a) is typical of the low-nutrient waters of the open ocean, the setting for much of 'Open Ocean'. The pair of food chains in (b) are typical of productive waters over the continental shelf – you may remember that 'Seasonal Seas' was concerned with temperate shelf waters. The pair of food chains in (c) are typical of the highly productive waters found in regions of upwelling. Before looking at Figure 5.11 in more detail, we should emphasise that although they are a good way to begin understanding how an ecosystem functions, food chains are often highly simplified representations of the feeding interactions in an ecosystem. In the real world, predator–prey relationships are usually complicated, with many carnivores feeding on a variety of prey, and themselves being prey for a variety of larger predators. As a result, feeding interactions in an ecosystem or community are more accurately represented by a food *web*, i.e. a number of interrelated food chains: an example of a simplified food web (for Arctic waters) can be seen in Figure 8.4.

At the left-hand ends of the food chains in Figure 5.11 are the primary producers, which make their own organic material (i.e. plants or, in some unusual circumstances, bacteria; Section 1.4, and beginning of Chapter 4). Then come the herbivores, which feed on plants, followed (in food chains (a) and (b)) by carnivores which feed on other carnivores. Primary producers are described as being at the lowest *trophic level* in the food chain, i.e. they are at trophic level 1 ('trophic' means 'relating to nutrition'). Herbivores are at trophic level 2, carnivores that eat herbivores are at trophic level 3, carnivores that eat carnivores are at level 4, etc. Carnivores that are not preyed on by any other animals are known as top predators. In reality, however, an animal with a mixed diet can occupy more than one trophic level. This may be a reflection of what food is available; to take a terrestrial example, bears which catch salmon during the summer salmon run may depend on berries later in the year.

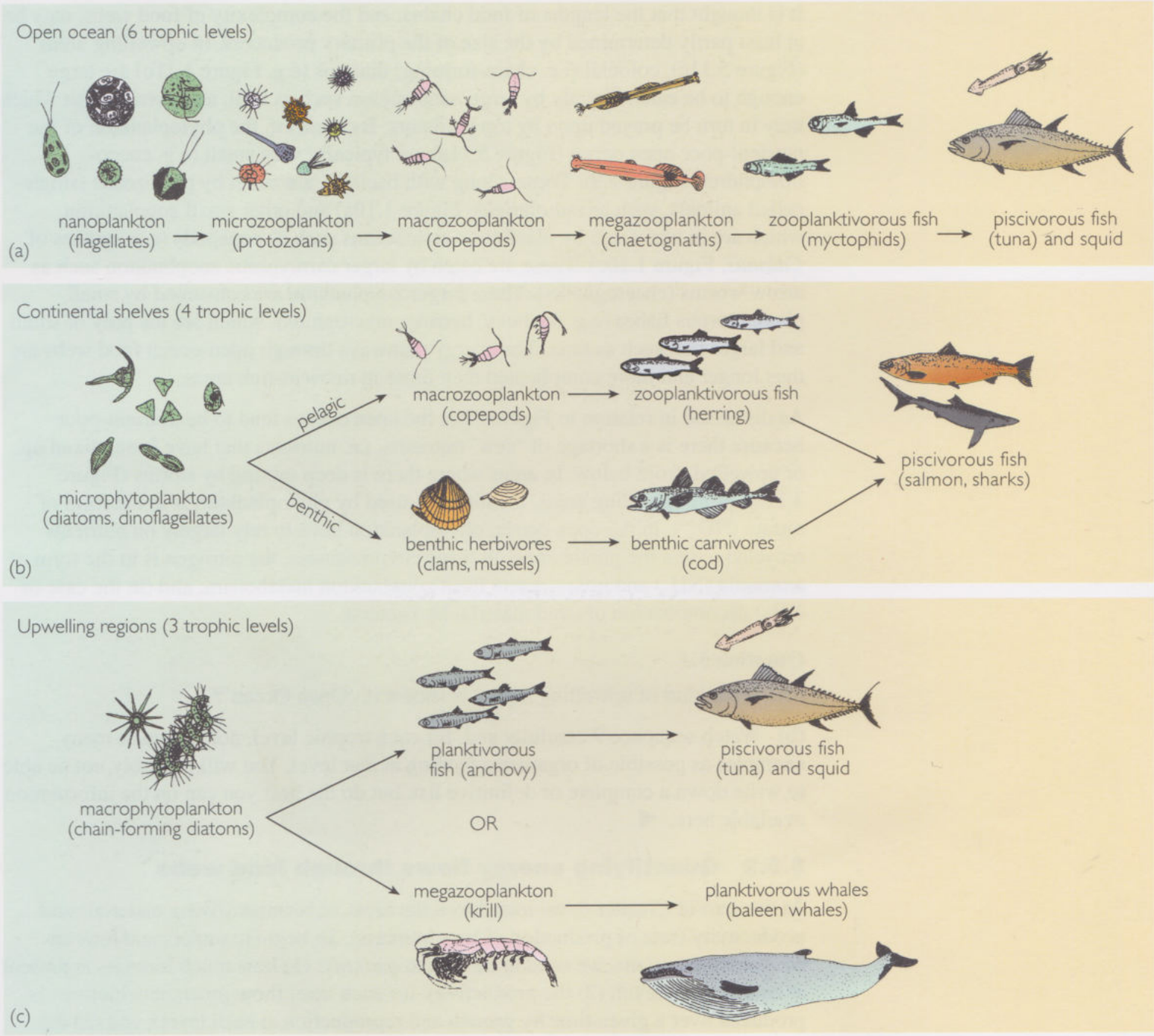


Figure 5.11 A comparison of food chains in three different marine habitats. *Note:* The organisms representing each trophic level are selected examples of the many marine species that could be present at that level. In (a), chaetognaths are arrow worms, and myctophids are small mid-water fish with bioluminescent organs, commonly known as lanternfish. Note also the prefixes indicating different size ranges: nanoplankton (the smallest phytoplankton) are 2–20 µm across (µm = micrometre, i.e. one-millionth of a metre, 10^{-6} m); microplankton are 20–200 µm across; macro- and megaplankton may be millimetres to centimetres across/long. Piscivorous fish are fish that eat other fish.

On the basis of the three food chains in Figure 5.11, would you say that the number of trophic levels in a food chain is related to the productivity of the region concerned? If so, how?

Yes. Figure 5.11 suggests that less productive regions such as the open ocean have longer food chains (i.e. food chains with more trophic levels), while more productive areas have shorter food chains (with fewer trophic levels). Upwelling areas have the shortest food chains of all.

It is thought that the lengths of food chains, and the complexity of food webs, may be at least partly determined by the size of the primary producers. In upwelling areas (Figure 5.11c), colonial (i.e. chain-forming) diatoms (e.g. Figure 1.11b) are large enough to be eaten directly by large zooplankton such as krill, and even by fish which may in turn be preyed upon by top predators. By contrast, the phytoplankton of the nutrient-poor open ocean (Figure 5.11a) are typically very small (e.g. coccolithophores, Figure 1.9). These, along with bacteria, are eaten by protozoans (single-celled animals, such as radiolarians; Figure 1.10a) and other small zooplankton, which are in turn eaten by planktonic crustaceans such as copepods (e.g. species of *Calanus,* Figure 1.10c). These are eaten by larger carnivorous zooplankton such as arrow worms (chaetognaths). These larger zooplankton are consumed by small planktivorous fishes (e.g. anchovy, herring, myctophids), which are the prey of squid and larger fish such as tuna. The energy pathways through open-ocean food webs are thus longer and more complicated than those in nutrient-rich areas.

As discussed in relation to Figure 5.6a, the open oceans tend to be nutrient-poor because there is a shortage of 'new' nutrients, i.e. nutrients that have been mixed up, or upwelled, from below. In areas where there is deep mixing by storms (Figure 4.11a), or in upwelling areas, the nitrogen used by phytoplankton is in the form of nitrate (NO_3^-). In the open ocean, phytoplankton have to rely largely on nutrients recycled *within* the photic zone. In these circumstances, the nitrogen is in the form of ammonia (NH_3) and urea – waste from zooplankton metabolism, and (in the case of NH_3) decomposition of dead material by bacteria.

Question 5.3

(a) What kind of upwelling region is shown in 'Open Ocean'?

(b) Watch sequence 7 carefully and, for each trophic level, note down as many examples as possible of organisms feeding at that level. You will probably not be able to write down a complete or definitive list, but do the best you can on the information available here. ◀

5.5.2 Quantifying energy flows through food webs

At the start of Chapter 4, we introduced the ideas of biomass (living material) and productivity (rate of production of new biomass). To begin to understand how an ecosystem functions, we need to be able to *quantify*: (1) how much biomass is present at each trophic level; (2) the productivity for each level (how much new biomass is produced over a given time by growth and reproduction at each level); and (3) the efficiency with which biomass at one level is converted to biomass at the next level up (known as trophic efficiency). With this information, we can make some deductions about how much biomass (and associated productivity) is needed at lower levels to support animals further up the food chain/web.

The difference between biomass and production can be well illustrated by considering the difference between land plants and plants in the sea. Estimates of the annual production of plants on land and plants in the oceans vary, but researchers agree that they are of the same order of magnitude. Nevertheless, at any one time the total *mass* of living material (or biomass) in land plants is at least 100 times that of plants living in the ocean (perhaps even 250–300 times, according to some estimates).

● By thinking about the difference between plants on land (particularly large plants) and plants in the sea, can you explain this?

- Much of the biomass of large land plants, notably trees and shrubs, is *non-growing* woody material which persists from year to year. The average lifetime of terrestrial vegetation is very long compared with that of marine plants (on average, about 18 years compared with 10–20 days for phytoplankton before they are eaten or die). So, compared with terrestrial vegetation, the 'turnover time' of marine vegetation is very short – a lot is produced each year, but none of it lasts long and so at any one time the total amount present is relatively small.

If we wanted to compare amounts of biomass, say that in one rock pool compared with another, we could (in theory at least) collect and weigh all the plants and animals in each pool. Even if we could do this, we would have a number of problems. To begin with, different organisms contain different amounts of water – a living jellyfish is nearly *all* water! To get round this problem, biomass is usually expressed in terms of grams (or kilograms) of carbon, gC (or kgC) (carbon accounts for a significant proportion of the (dry) body weight of all organisms). To deal with the fact that the two pools might be different sizes, we would calculate the biomass per unit area of the pool (e.g. per square metre or per square centimetre). Typical units of biomass would therefore be gC m^{-2} or gC cm^{-2}. The same is often done to express the biomass of phytoplankton, zooplankton, or particular fish in an area of ocean, or the biomass of (say) echinoderms on the deep sea-bed. Productivity (rate of production of new biomass per unit time) is typically expressed in gC m^{-2} day^{-1} or gC m^{-2} $year^{-1}$. Sometimes, particularly where an ecosystem occupies a fairly well-defined area of sea (e.g. a shelf sea or a sea within an arc of islands), the quantities used are those for the entire area. In such cases, biomass is often expressed in kilotonnes or megatonnes (10^3 t and 10^6 t) of carbon, i.e. ktC and MtC, and productivity is expressed in ktC $year^{-1}$ and MtC $year^{-1}$. Using weights of carbon may seem rather abstract; to convert to weight of live organisms (or organisms that were recently alive), we can use the approximate relationship that 1 gC represents 10 g live/fresh weight (i.e. the weight expressed in terms of units of carbon is one-tenth of the live weight in those units).

The term 'ecosystem' (which we have been using fairly loosely) means all the interdependent communities of organisms in a particular geographical area, plus the physical environment that they inhabit (although in some circumstances it is used more generally, as in 'marine ecosystem'). As you might imagine, making estimates of productivity (over, say, a year) for a particular ecosystem is very much more complicated than estimating the biomass in a rock pool at one particular time. Apart from the technical challenges, there would be practical problems associated with the behaviour of the animals themselves.

- Can you suggest some examples of such behaviour, illustrated in all of the Blue Planet programmes?

- The biggest problem is that most animals do not stay still! Even a rock pool has a varying population, which changes over the course of the tidal cycle, and over the course of the year. More generally, many animals have migratory life cycles, belonging to different ecosystems at different stages of their lives. Another problem is that animals are not evenly distributed – even in the open ocean they tend to have patchy distributions, which might be continually changing in a fairly random way (e.g. in response to currents).

Now let's return to Figure 5.11c. If we make the simplifying assumption that the two food chains are independent from one another (e.g. that the baleen whales do not consume any small fish), we can split this 'double food chain' into two separate food

chains, as follows:

Food chain 1: diatoms → planktivorous fish (e.g. anchovy) → piscivorous fish

Food chain 2: diatoms → krill → baleen whales

If we make an assumption about how much of the primary production (the diatoms) is consumed by the planktivorous fish, and how much is consumed by the krill, we can make estimates of the increase in biomass of piscivorous fish and whales that can be supported by the diatoms. In order to do this, we need to know the efficiency with which biomass at each level is converted to biomass at the next level up, i.e. what proportion of an animal's food is converted into new tissue through growth and reproduction. Krill are very energetic animals, and have comparatively high metabolic rates, so they need a lot of 'fuel'. They use the equivalent of about 5% of their body weight per day just to stay alive, i.e. for respiration/metabolism. Furthermore, not all the food they consume is digested, absorbed and used; a significant proportion is lost as faeces. All this means that krill convert phytoplankton tissue to krill tissue with an efficiency of 10–15%; in other words, for every 100 g of phytoplankton consumed, there is an increase in krill biomass of only 10–15 g. The precise value would depend on how good feeding conditions are for the krill. For example, if phytoplankton are scarce, krill have to use up more energy collecting them, with the result that feeding is less efficient, and conversion of phytoplankton biomass into krill biomass is effectively *also* less efficient.

More generally, the efficiency with which animals convert the food they have eaten into new tissue depends on what the food is and the metabolism and life style of the animal. Trophic efficiencies between phytoplankton and herbivorous zooplankton are generally about 20%, while trophic efficiencies between zooplankton and fish, and fish and larger fish, are generally about 10%. However, baleen whales convert krill biomass into whale biomass much less efficiently, at about 4%.

Thinking back to Section 2.1.2, can you explain this low efficiency?

Whales are mammals, and so are warm-blooded, maintaining a constant body temperature which is often more than 30 °C higher than that of the surrounding water. If they are to generate sufficient heat to achieve this, their metabolic rate needs to be high, which in turn means that they use a large proportion of their food as fuel, with the result that there is less available for growth.

Using some typical efficiencies, we can now begin to quantify the flow of energy along our two food chains:

Food chain 1: diatoms $\xrightarrow{0.1}$ planktivorous fish $\xrightarrow{0.1}$ piscivorous fish

Food chain 2: diatoms $\xrightarrow{0.12}$ krill $\xrightarrow{0.04}$ baleen whales

The numbers over the arrows are the efficiencies, expressed as decimals rather than percentages, i.e. 0.12 = 12%, 0.1 = 10%, and 0.04 = 4%. (If you are unsure about decimals and percentages, refer to the *Maths Skills Booklet*.)

For convenience, let us assume that our two food chains represent the main trophic relationships in a hypothetical upwelling area, with an annual primary production of about 100 MtC year^{-1}. If we make some assumptions about the way this annual primary production is shared between the two food chains, we can make an estimate of the annual production (growth and reproduction) of piscivorous fish and baleen whales it could sustain. So, let's assume that the krill and the planktivorous fish

(anchovy etc.) each consume half of the annual production of diatoms (50 MtC). To calculate the annual production of piscivorous fish, all we need to do is multiply the annual primary production available to the food chain by the efficiencies along food chain 1, as follows:

$$\text{annual production of piscivorous fish} = 50\ \text{MtC} \times 0.1 \times 0.1 = 0.5\ \text{MtC}.$$

(Note that whatever units the primary production was quoted in, these are automatically the units of the production of piscivorous fish.)

Question 5.4

(a) Using the method illustrated above, calculate the annual production of whales in our upwelling area, also in MtC. Hence calculate the total annual production of carnivores in the area. What would this be in terms of live weight?

(b) Here is the food chain in Figure 5.11a, along with typical trophic efficiencies:

$$\text{nanoplankton} \xrightarrow{0.25} \text{microzooplankton} \xrightarrow{0.15} \text{macrozooplankton} \xrightarrow{0.1}$$

$$\text{megazooplankton} \xrightarrow{0.1} \text{zooplanktivorous fish} \xrightarrow{0.1} \text{piscivorous fish/squid}$$

The annual primary production in a region of open ocean would be a fraction of that in an upwelling area, perhaps ~ 20 MtC.

(i) Again using the method illustrated above, use this information and the food chain above to estimate the annual production of piscivorous fish/squid in an area of open ocean. (Express your answer in MtC and ktC.)

(ii) How does your answer compare with the total annual production of carnivores in the upwelling area, which you calculated in part (a)? (Here we are comparing the production of top carnivores in the two areas, according to the food chains shown.) ◀

You may have been wondering why we have been implicitly assuming that most or all of the primary production will be eaten – would it not be possible for it to remain uneaten, and die naturally? The answer is that an 'ecosystem' is just that – an ecological *system* in which the various components are not independent, and changes in one component will result in changes in other components of the system. An increase in the availability of phytoplankton will allow herbivorous zooplankton (krill and other animals) to grow and reproduce at a greater rate; if the phytoplankton population goes into decline, the population of zooplankton will also go into decline.

- Bearing in mind what you read towards the end of Section 4.3, can you identify particular circumstances under which large numbers of dead phytoplankton sink from surface waters (i.e. without having been digested first)?

- Dead/dying phytoplankton will sink from surface waters when there is a lag between increases in phytoplankton populations and increases in the zooplankton that feed on them, with the result that for a short time there are more phytoplankton than can be consumed. This is particularly the case in the northern North Atlantic during the spring bloom.

As you will see in Chapter 10, the great abundance of dead phytoplankton that escape from surface waters during the spring bloom has an important impact on life on the sea-bed beneath (as well as the waters in between). This illustrates why a proper understanding of life in the seas and oceans will only be possible if we remember that individual ecosystems are by no means independent of one another, and that the

concept of 'marine ecosystem' – encompassing life in the water column and on the sea-bed, in coastal environments, shelf seas and the deep sea – is very valuable. How true this is will become clear later on, particularly in the final chapter, where we look at the perilous state of fish stocks world-wide.

Question 5.5

As mentioned in Section 5.5.1, an animal with a mixed diet can occupy more than one trophic level in a food web.

(a) What two trophic levels does the rorqual in the centre of the Arctic food web (Figure 8.4) occupy, and why?

(b) Thinking back to the sequences about tuna in 'Open Ocean' (sequences 1, 3, 4 and 7), and bearing in mind the answer to Question 5.3b, can you suggest another way in which an animal may be described as being at more than one trophic level? ◀

Question 5.6

The format of this question is similar to that of some of the ECA questions. To get some practice in answering such questions, we suggest that you write your answer out in full (rather than just making notes), and then compare it with ours.

Gelatinous zooplankton are very beautiful, and so feature prominently in many of the Blue Planet programmes (particularly 'The Deep'). However, with the exception of species living in near-surface waters, very little was known about them until relatively recently, and it is not at all clear how their biomass varies and how important a role they play in food webs.

(a) (i) Name at least two groups of gelatinous zooplankton shown in the Blue Planet programmes you have seen so far, from at least two different phyla. Name the phylum in each case.

(ii) Can you suggest why it is an advantage to these animals to be gelatinous? (*One or two sentences*)

(b) Why do you think these animals are so hard to study, both in terms of their life processes and their role in food webs? (*Three or four sentences*)

Note: The answer to part (b) is not given explicitly in the course, and there is no single 'right answer'. We are looking for sensible suggestions based on information that *is* in the course. ◀

Question 5.7

What top predator did you see in the introductory programme? ◀

Fish design

6

In previous chapters, we have been examining the various factors that affect the oceanic environment – light levels, the shape of the sea-bed, mixing, currents and nutrient concentrations – and we considered how these factors influence biological productivity in various parts of the ocean. In this chapter, we will be concentrating on one group of animals – fish – and look in particular at how fish swim and at their buoyancy. The subject of how fish swim is also covered in the two programmes which accompany this chapter (on DVD 2). However, marine mammals are not completely neglected because the second of these programmes also looks at what makes dolphins particularly good swimmers and sperm whales such efficient divers.

6.1 Different classes of fish

Fish come in an enormous variety of shapes and sizes, depending on where and how they make their living. Fish are craniates (i.e. vertebrates) and most belong to the Class Osteichthyes ('bony fish'). The two other classes of fish found in the oceans are the Agnatha and the Chondrichthyes (and for completeness, we should mention the 'lungfish' which live only in freshwater). Agnatha means 'without jaws': rather than biting by using hinged jaws, agnathans feed by rasping. Today, there are only two types of jawless fish: lampreys (which live in marine and freshwater environments); and the wholly marine hagfish, which you will see in action in 'The Deep'. Chondrichthyes means 'cartilaginous fish' (chondro = relating to cartilage). Of the cartilaginous fish – also known as *elasmobranchs* – the best known are the sharks and rays.

In fact, hagfish also have cartilaginous skeletons, but they clearly belong to a more primitive group than the chondrichthyes. The jawless fish were the first vertebrates, and appeared during the Cambrian Period (Section 1.1). Along with two other groups of fish (now extinct), they became very diverse during the Devonian, often known to palaeontologists as the 'Age of Fishes' (partly because fish were the only vertebrates then flourishing).

It is thought that jawless fish, elasmobranchs and bony fish have been evolving along separate paths since the late Ordovician (cf. Figure 1.1). Jawless fish declined markedly during the Carboniferous and never recovered. Both elasmobranchs and bony fish were hit hard during the mass extinction at the end of the Permian, but have diversified since then. Bony fish in particular have become extremely diverse over the course of the last 65 million years (i.e. during the Cenozoic Era; Figure 1.1). In modern seas, most bony fish (and hence the great majority of the more than 22 000 species of marine fish) are *teleosts*, or 'complete bones'. Teleost fishes have adapted to live in an enormous variety of different environments, in freshwater, shallow marine waters, the open ocean and the deep sea.

Because of their different evolutionary histories, elasmobranchs and teleosts have many differences, some more obvious than others.

Question 6.1 Think back to the various Blue Planet sequences showing sharks, for example the blue shark, hammerhead sharks, white-tip reef sharks and the silke shark in 'Open Ocean' (sequences 4 and 7). Can you name at least three distinctive physical features that seem to be characteristic of sharks? ◀

Some of the most notable contrasts between elasmobranchs and sharks are as follows:

- Teleosts have bony skeletons, with many more separately moveable parts than the skeletons of elasmobranchs, which are made of cartilage (a firm elastic tissue which, unlike bone, is not calcified).
- Teleosts have evolved a variety of jaw mechanisms, allowing a great diversity of feeding habits and diets. (The Blue Planet programmes – especially 'The Deep' – provide some striking examples of jaws adapted to allow survival in particular ecological niches.)
- Most teleost fishes have neutral buoyancy (i.e. they tend to neither sink nor rise in the water column) mainly as a result of having a swimbladder. Elasmobranchs do not have a swimbladder, although some species come close to achieving neutral buoyancy as a result of having large livers which store considerable amounts of oil. (Buoyancy will be discussed in Section 6.3.)
- Elasmobranchs are typically good swimmers, but their manoeuvrability is limited and they cannot swim backwards or hang motionless in the water as many teleosts can.
- Elasmobranchs produce small numbers of relatively large yolky eggs. Fertilisation is internal and the eggs are either laid in protective cases or retained in the mother's body until they are ready to be born. In some elasmobranch species, embryos are fed by the mother while they are developing inside her. In contrast, the vast majority of teleost species lay large numbers of small eggs that float in the water and are fertilised externally. They hatch into tiny larvae which join the meroplankton.

You may remember the baby dogfish growing in its egg capsule attached to a strand of kelp, towards the end of 'Seasonal Seas' (sequence 13). On the basis of this sequence, would you say that dogfish are teleosts or elasmobranchs?

The egg capsule, and the hatching of a fully developed fish rather than a fish larva, both tell us that dogfish are elasmobranchs.

In 'Open Ocean', we effectively followed the life of a yellowfin tuna, from egg to young adult.

Do you think that tuna are teleosts or elasmobranchs?

They are teleosts. As shown in sequence 3, tuna develop from large numbers of small eggs that have been released to float in the ocean.

We suggested that, while watching 'Open Ocean', you made a note of any characteristic features of fast-swimming fish like tuna (or indeed marlin, mackerel, trevally etc.), paying particular attention to the body shape and shape of the tail. Later in the next section, you will be able to compare your notes with our illustrations.

6.2 Fish shape, fins and tails

In all fish, the main body of muscles is arranged in distinct overlapping segments or layers, situated on either side of the spinal column and enclosing the body cavity which contains the stomach, liver, intestines etc. These overlapping layers of muscle make up the white or light-coloured flesh used in many fish dishes: when fish is lightly cooked, the muscle segments can be easily separated. Perhaps surprisingly, in most fish species living in the upper 500 m or so of the ocean (i.e. the fish with which we are most familiar), this white muscle is used only in fast 'bursts' of swimming.

For normal cruising speeds (i.e. during steady energy-efficient swimming), these fish use a thin layer of red or brown muscle (which is also in a series of segments) situated along the flanks close to the skin.

Now imagine the type of swimming seen in eels (*Anguilla anguilla*) and some fish larvae. Here, the animal moves forward as a result of a succession of waves moving down the body from head to tail (Figure 6.1). The bending of the body in the backward-travelling wave is achieved by muscle contractions on one side of the spinal column being accompanied by relaxation and slight stretching of muscles on the other side. Because the bent portions of the body wall push against the water, as the wave moves backwards the animal is propelled forwards. The final thrust is provided by the tail.

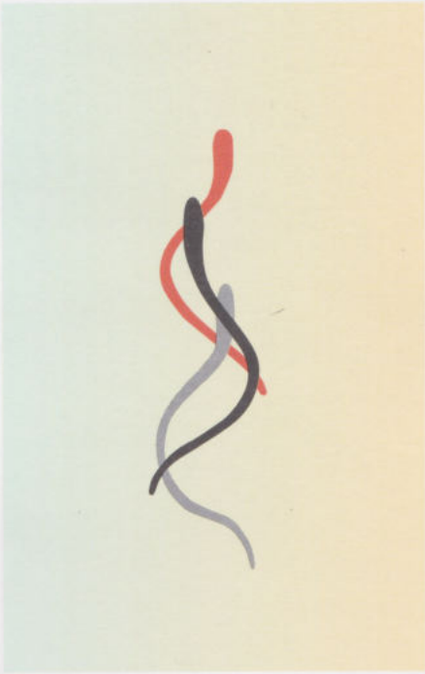


Figure 6.1 The mode of swimming used by the eel (seen from above). The grey, black and red silhouettes show the eel at intervals of 0.3 seconds.

Thinking back to 'Open Ocean', would you say that tuna and marlin swim in this manner?

No, the bodies of these fish remain quite stiff during swimming, while the large tail moves vigorously from side to side, generating the thrust which propels them forward.

In the case of tuna, the major body muscles deliver the propulsive force to the tail by means of large tendons which pull the tail from side to side on a hinged joint. This contrasts with the eel-like style of swimming, which is very inefficient as a lot of energy is expended on side-to-side movement of the head and body, as well as of the tail. Most fish have a mode of swimming which is intermediate between these two extremes.

A fish moving through water experiences a force opposing its motion. This force, known as drag, is approximately proportional to the *square* of its speed in relation to the water.

So what will happen to the drag experienced by a swimming fish if it trebles its speed?

The drag will become nine times greater. (As the swimming speed increases 3-fold, so drag will go up by $3^2 = 3 \times 3 = 9$-fold.)

This illustrates how important it is for swimming animals to keep drag as low as possible. The total drag acting on a swimming animal is made up of two components: *pressure drag*, which is the opposing force experienced as it 'pushes' its way through the water, and *skin friction drag*, which is the frictional force generated by the water moving over the surface of the animal. Pressure drag is reduced by having a long, thin body with a pointed front. However, long thin shapes have a large surface area relative to volume, and this increases skin friction drag. For fast swimming, therefore, a compromise is needed. It will probably not surprise you to learn that the smallest possible total drag is achieved by having the torpedo-like shape of fast-swimming fish like tuna, as well as many whales and dolphins. Pressure drag and skin friction drag are described in 'Wild Moves: Water'.

Drag can be further minimised by increased streamlining through reduction of protuberances on the body. Some fish, including tuna, can fold their fins into grooves and recesses on their bodies. Even the eyes of tuna are flush with the head and covered with a layer of fatty tissue.

In the case of a streamlined fish swimming at low speeds, the flow of water around the body is smooth and laminar, i.e. in layers. The thin layer of water adjacent to the

surface of the fish moves *with* the fish, and each succeeding layer is influenced by the motion of the fish slightly less. So if the fish were swimming through still water, the layer of water closest to the fish would move at the speed of the fish, the next layer out would move slightly slower, the next one out again would move even more slowly, etc. This situation results in low drag. If the fish speeds up, there will come a point when the smooth flow of water over its body begins to break down and turbulent eddies start to be generated. The onset of turbulence results in about a three-fold increase in drag, and fish that need to swim fast have strategies to delay this, which include keeping side-to-side motion to a minimum (as noted above). Only slow-swimming fish make large side-to-side movements. In the case of tuna, the little fins on the slender part of the body near the tail are thought to help delay the onset of turbulence.

The skin of the fish may itself be adapted to reduce drag. The skins of some fish species produce mucus, which helps reduce friction and promotes laminar flow. This is probably most effective at slow speeds. By contrast, the scales of some fish, such as sharks, have tiny tooth-like protuberances which generate small vortices or eddies, producing a layer of 'microturbulence' which acts as a kind of lubricant, reducing friction and delaying the onset of fully developed turbulence. (This principle has been adopted by designers of racing yachts and suits for competitive swimming.) Some marine fish have a porous skin so that seawater can pass into and out of a 'canal' system just under the surface; this can also help to produce a layer of microturbulence close to the skin.

Fishes make forward progress against drag by generating thrust. Just as jet engines expel hot gases backwards in order to move forward, so fish send 'parcels' of water backwards to propel themselves forward. In fact, the water sent backwards by a swimming fish bears more resemblance to the vortices sent back from a propeller than to the jet from an engine (Figure 6.2). A tail beat to the right generates anticlockwise vortices (seen from above in Figure 6.2a), and a tail beat to the left generates clockwise vortices. The amount that a fish moves forward as a result of one to-and-fro sweep of the tail is known as its 'stride-length'. In most normal fish, one stride-length is about 0.7 of the length of the fish.

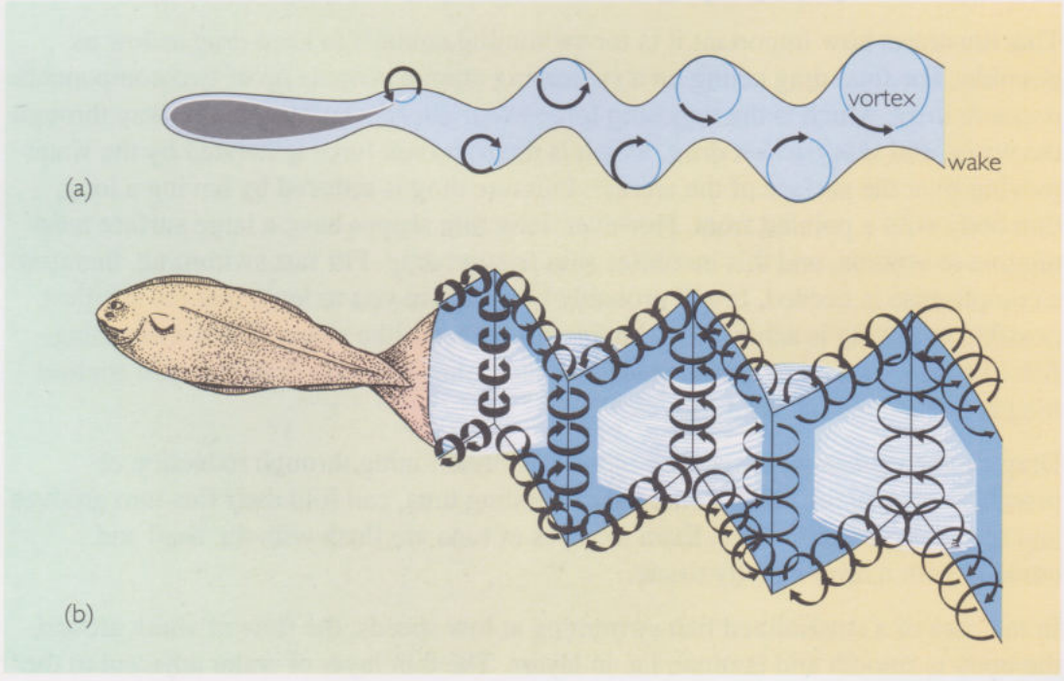


Figure 6.2 (a) A two-dimensional view of the wake of a swimming fish viewed from above, showing the vortices released at the end of every stroke of the tail to the right or left. (b) An impression of the vortex flow system behind a swimming fish, seen from the side. The tail is shown in the middle of a stroke towards you. The 'tightness' of the vortices and the speed of the water flow (indicated by the thickness of the arrows) decrease as they spiral out behind the fish.

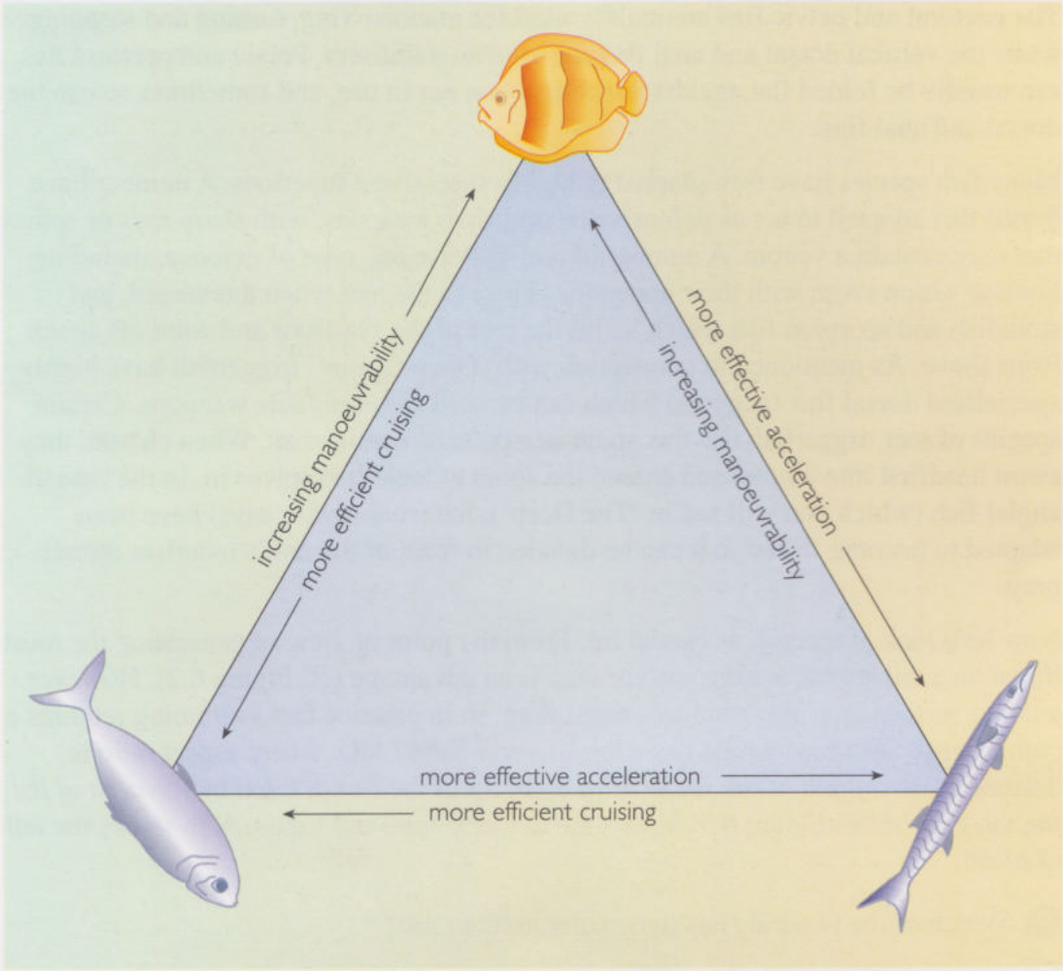


Figure 6.3 The 'fish triangle', showing ideal shapes for efficient cruising (torpedo-like), good acceleration (low drag, but well-muscled), and manoeuvrability (disc-shaped and flattened). Most fish have a body shape that is a compromise between these three extremes.

For many fish, habitat and lifestyle mean that being able to cruise efficiently is not a high priority. Instead, they may need to accelerate quickly, or be able to manoeuvre well. Fish that specialise in short bursts of speed (for striking at prey or escaping from predators) are generally long and thin, which (as mentioned above) maximises the surface area in contact with the water and so also maximises the thrust that can be generated by the body. These darting fish also have a lot of muscle relative to their size (making them rounded rather than oval in cross-section) and have strong tails. Fish that specialise in quick turns are somewhat flattened and disc-shaped, which gives them a more flexible body. Most fish species have a shape that is a compromise between these three extremes (Figure 6.3), but there are also specialists, such as plankton-feeders and those that hunt by stealth and rely on camouflage, and these may have very bizarre shapes indeed. (You will see some good examples of this last category in 'Coral Seas'.)

Fins also play an important role in swimming and turning, and are supported and moved by means of fine flexible rods or spines known as fin-rays, or simply rays. Fish generally have a pair of pectoral fins (one either side, behind the head), two dorsal fins along the back, an anal fin beneath the rear half of the body, a pair of pelvic fins on either side of the lower body (forward of the anal fin), and a caudal (tail) fin (Figure 6.4). The size, shape and position of these fins varies greatly between species, and in certain species some types of fin may be absent altogether.

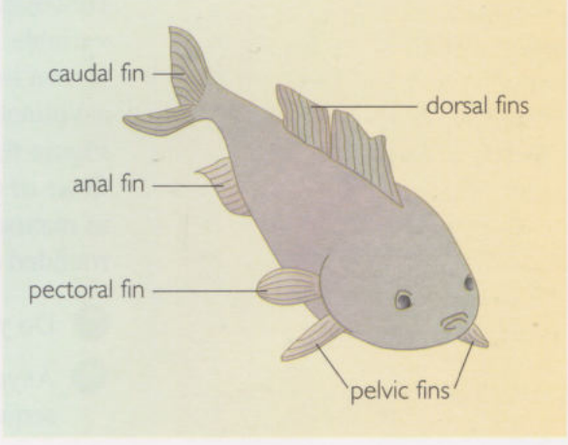


Figure 6.4 The different types of fins, shown on an imaginary fish.

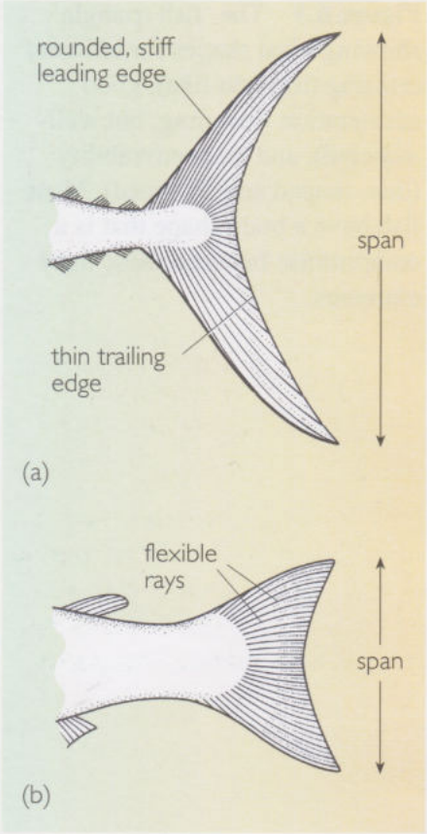


Figure 6.5 Two similarly shaped tails of different aspect ratios: (a) is a tuna (note the small fins just forward of the tail, which are thought to delay the onset of turbulence), and (b) is a cod.

The pectoral and pelvic fins are mainly used for manoeuvring, turning and stopping, while the vertical dorsal and anal fins are used as stabilisers. Pelvic and pectoral fins can usually be folded flat against the body when not in use, and sometimes so can the dorsal and anal fins.

Many fish species have fins adapted to highly specialised functions. A number have dorsal fins adapted to act as defensive or offensive weapons, with sharp rays or spines that may contain a venom. A number of reef fish use this type of defence, including lionfish which swim with their undersides close to the reef when threatened, and stonefish and scorpion fish which lie on the reef or the sea-floor and ward off attack from above. As mentioned in connection with 'Open Ocean', triggerfish have highly specialised dorsal fins (triggers) which can be used as formidable weapons. Certain species of reef triggerfish use this spine as a defence mechanism. When chased, they swim headfirst into a hole, and extend the spine to lock themselves in. In the case of angler fish (which you will see in 'The Deep'), the front ray (or rays) have been adapted to become 'lures' that can be dangled in front of the fish's mouth to attract prey.

Now let's look at the tail, or caudal fin. From the point of view of generating the most thrust on a tail stroke, a large surface area is an advantage (cf. Figure 6.2). However, a larger surface area also produces more drag, so in practice fast swimming requires a compromise tail shape which has a large *aspect ratio* (AR), where aspect ratio is defined as the *square of the span* (from tip to tip of the fin) divided by the *area of the fin*, i.e. span^2/area. Figure 6.5a shows the tail of a tuna, and Figure 6.5b shows the tail of a cod.

Which of the two tails has the greater aspect ratio?

Not surprisingly, it is that of the tuna.

Relatively speaking, the area of the tuna tail is somewhat bigger than that of the cod, but the span, and especially the *square* of the span, is a lot bigger, making span^2/area significantly bigger. Tuna tails have an AR of about 6, which is as high as it can be before strength begins to be sacrificed. Broader, low AR tails, like those of cod, are more suited to slow speeds, and good acceleration from a 'standing start'. Note, however, that fish can to some extent *change* the aspect ratios of their tails to suit the speed, by separating the rays of the fin or bringing them together. (Blacksmith fish could be seen changing the shapes of their tails in 'Seasonal Seas' (sequence 4).)

However, swimming fast is not always the main requirement, so tail fins are highly variable in shape. For ease of discussion, we can divide them into five main types, as shown in Figure 6.6: rounded, truncate, forked and lunate ('moon-shaped'), plus asymmetric (see below). The aspect ratios of these tails increase from left to right in Figure 6.6 (i.e. from rounded to lunate), and as mentioned above, lunate tails like those of tuna provide good thrust. However, they are very stiff, and provide little help in manoeuvring, so although a predatory tuna could easily outswim a fish with a rounded or truncate tail, the prey might well escape by outmanoeuvring the tuna.

Do you recognise the type of tail shown at the far right?

Asymmetric tails are typical of sharks and dogfish (as shown, for example in sequence 7 of 'Open Ocean' and sequence 13 of 'Seasonal Seas').

Asymmetric tails have a special function, discussion of which is reserved to the next section.

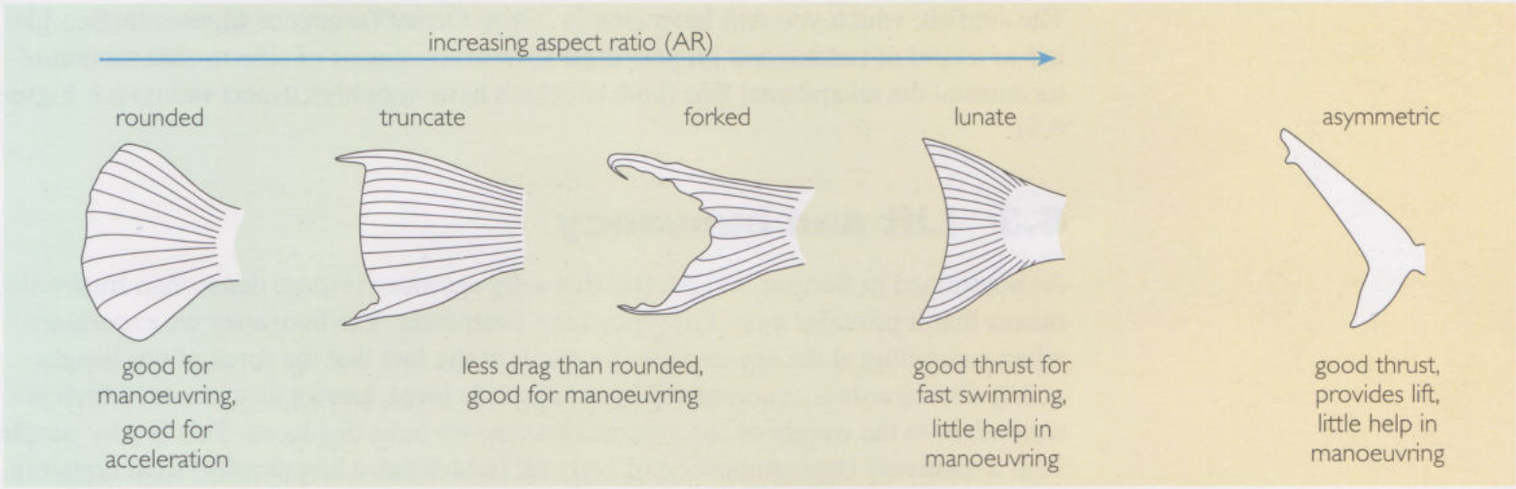


Figure 6.6 The five basic types of tail fin, the first four arranged in order of increasing aspect ratio. Many fish species have tail shapes that fall between these categories.

Some fish have fins that undulate (i.e. have a wave-like motion), which are used either as the main method of propulsion – as in the case of sea-horses, for example – or as an extra method, in addition to movement of the tail and body (Figure 6.7). Use of undulating fins confers excellent manoeuvrability. The 'wings' of rays are greatly enlarged pectoral fins, and rays propel themselves along by means of undulations passing back along the margins of the fins (as demonstrated by the bat ray in sequence 6 of 'Seasonal Seas'. (There are also some good examples of propulsion by undulating fins in 'Coral Seas'.)

Question 6.2 In Figure 6.7, the fins that undulate are toned in red (with the exception of the ray). Referring to Figure 6.4 as necessary, identify the type of fin involved in each case. ◀

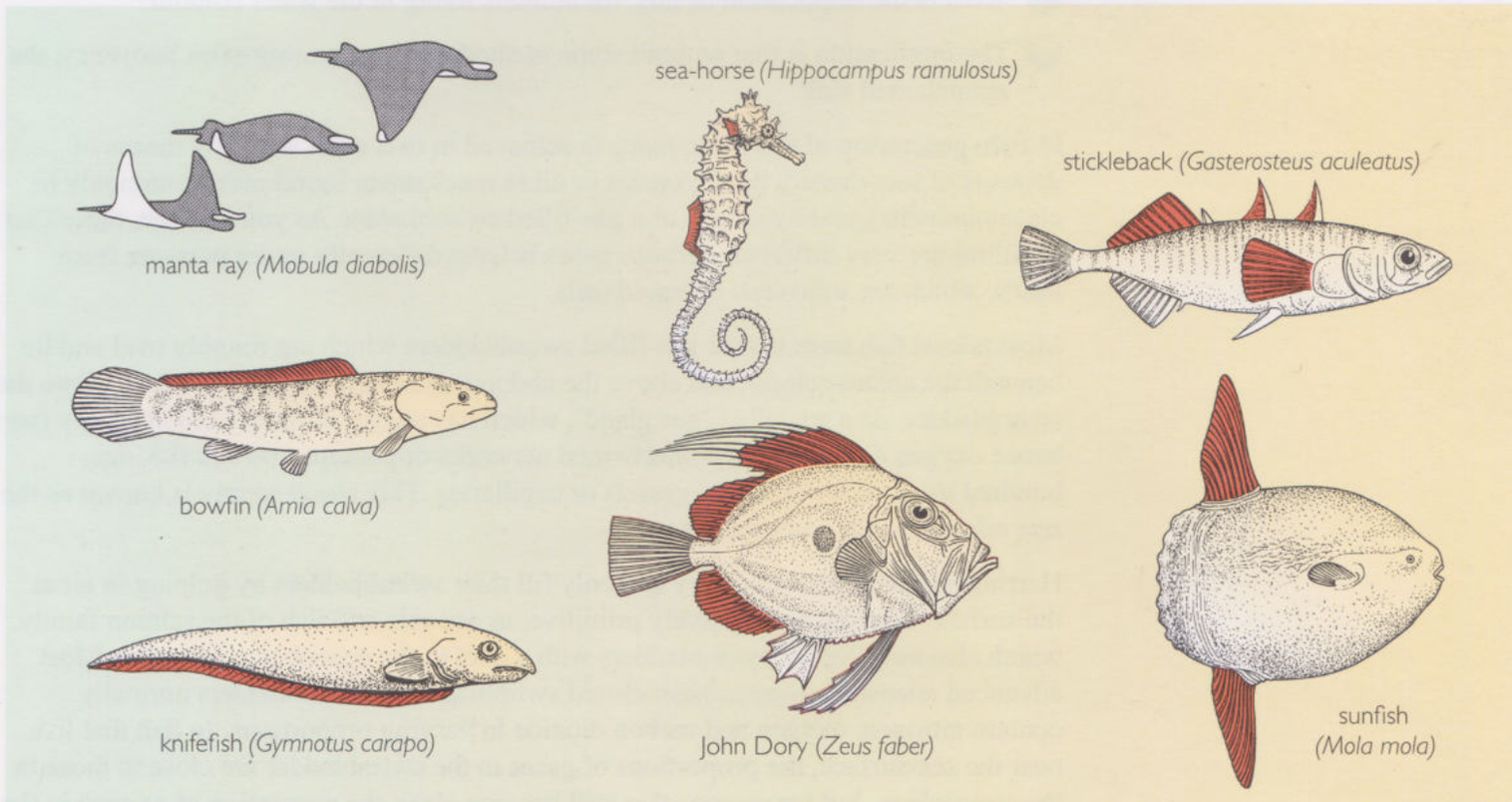


Figure 6.7 Examples of fish that use undulating fins for locomotion (the fins in question are shown in red). The fish are not shown to scale: sea-horses are only centimetres long, while sunfish may be 4 m from fin tip to fin tip.

The sunfish, which you will have seen in 'Open Ocean'(sequence 6), uses its flap-like tail as a kind of rudder, and propels itself forward by means of side-to-side motion of its unusual dorsal and anal fins (both of which have very high aspect ratios) (cf. Figure 6.5).

6.3 Lift and buoyancy

As mentioned in Section 2.1, the fact that salty seawater is more dense than freshwater means that it provides more buoyancy than freshwater. The buoyancy we experience when swimming at the sea-surface is a result of the fact that the force of our weight acting downwards is counteracted by an upwards force, known as upthrust, which is equivalent to the weight of the volume of water we have displaced. This is why people with a relatively large proportion of body fat (which has a low density) float higher in the water than people with little body fat – they do not have to displace as large a volume of water to generate sufficient upthrust to balance their weight.

Of course, most marine animals spend their lives completely submerged, so the volume of water that they displace is always the volume of their body. Their effective weight in water is their actual weight minus the weight of seawater they displace, i.e. minus the upthrust. To be neutrally buoyant (i.e. to be effectively weightless), and neither rise nor sink in the water column, they need an average density that is equal to the average density of the water they are in. For most fish, average body densities are reduced to some extent by the fact that the salt content of their blood is only 30–50% of that of seawater (Section 2.1.2). However, most animal tissues – notably bone and muscle – have a density that is greater than that of seawater (i.e. a cubic centimetre of bone or muscle weighs more than a cubic centimetre of seawater).

What is the implication of this, for animals living in the water column?

The implication is that without some method(s) of generating extra buoyancy, the animals will sink.

In fish, generation of extra buoyancy is achieved in two main ways: by means of deposits of low-density lipids, i.e. fat or oil (a mechanism found more commonly in elasmobranchs), and by means of a gas-filled swimbladder. As you will see, these two solutions are very different, because gases behave differently under pressure from lipids, which are solid (fat) or liquid (oil).

Most teleost fish have elastic gas-filled swimbladders which are roughly oval and lie beneath the spinal column and above the abdominal cavity. Oxygen is released into the swimbladder via a so-called 'gas gland', which has an extraordinary blood supply (and hence oxygen supply) of two intertwined networks of perhaps 100 000 (i.e. one hundred *thousand*) tiny blood vessels or capillaries. This blood supply is known as the *rete mirabile* – the 'miraculous net'.

Herring are unusual in that they can only fill their swimbladders by gulping in air at the surface. Herring are relatively primitive, as are eels and fish of the salmon family, which also have 'open' swimbladders with a duct to the oesophagus or gullet. Most advanced teleosts, however, have closed swimbladders. Swimbladders normally contain nitrogen, oxygen and carbon dioxide in varying proportions. In fish that live near the sea-surface, the proportions of gases in the swimbladder are close to those in the atmosphere, but for reasons that will become clear, the proportion of oxygen in the swimbladder increases with the depth at which the fish lives, and the swimbladders of deep-sea fish contain almost pure oxygen.

Having a closed swimbladder imposes constraints on how fast and how far it is possible to swim up and down the water column. In gases, the constituent molecules are widely spaced, with the result that – in contrast to liquids and solids – gases are very compressible. The volume occupied by a given mass of gas can therefore change greatly in response to changing pressure, becoming smaller under increased pressure, and larger under reduced pressure. (You might remember the stream of bubbles rising from the shoal of herring being driven up towards the surface by killer whales in sequence 17 of 'Seasonal Seas' – as the pressure on the herring decreased, the air in their swimbladders expanded and escaped through their mouths.)

For a fish with an elastic swimbladder (containing a fixed amount of gas), what danger might there be in swimming rapidly up through the water column?

As the fish swam upwards, the pressure acting on it would decrease, and the volume of the gas-filled swimbladder would increase. This in turn would reduce the average density of the fish as a whole, making it still more buoyant, and causing it to rise faster. (Such a situation is known as a 'runaway positive feedback effect'.)

This expansion of gas under the influence of decreasing pressure is the reason that the swimbladders of fish caught at depth and brought rapidly to the surface using long lines or trawls, often explode or can be seen protruding from their mouths. The reverse problem would arise if our hypothetical fish swam downwards – its swimbladder would be compressed, the average density of the fish as a whole would increase, and it would sink still further.

Maintaining neutral buoyancy despite changing depth can be achieved by varying the amount of gas in the swimbladder so that its volume remains constant, regardless of the external pressure acting on the elastic swimbladder. The total amount of gas in the swimbladder may be increased by supplying extra oxygen from the blood, and, as you will probably have realised, this is where the gas gland and the *rete mirabile* come into play. The mechanisms whereby the oxygen content of the swimbladder is regulated are very complicated and we cannot go into them here. One aspect we *can* look at is how oxygen can pass into the swimbladder simply by *diffusion* from the *rete mirabile*, i.e. individual oxygen molecules passing from high-oxygen blood to a lower-oxygen swimbladder *without* being pumped in, even though the pressure in the swimbladder is very high. At first sight this does indeed seem miraculous!

Can you suggest why the networks of thousands of tiny capillaries allow the *rete mirabile* to supply oxygen so efficiently?

It is the large surface area of the mass of tiny capillaries, or strictly the large diffusion area in comparison with the volume of blood in the capillaries.

If you have ever gutted fish, you will have seen swimbladders, though perhaps without realizing what they were. Sometimes they have not completely collapsed, and sometimes (as in the case of herring, for example) they are easy to spot as they appear silvery. This is because they are covered by a continuous layer of overlapping crystals of a substance known as guanine. The crystals themselves are impermeable, and as they overlap, and lie closely together, any escape of gas occurs only very slowly. Even when the surface of the swimbladder is stretched or contracts, the overlapping crystals provide an effective barrier to gas escape.

Question 6.3 Some marine animals, including cuttlefish (*Sepia*), do not have swimbladders that can vary in size. Instead, the gas is effectively enclosed in a rigid 'box'. Can you suggest (1) any advantages, or (2) any disadvantages of this? ◀

As mentioned earlier, the other method of generating extra buoyancy, found more frequently in elasmobranchs such as sharks, is the accumulation of low-density lipids. Ordinary fish oils (e.g. cod liver oil) have densities of around 930 kilograms per cubic metre (kg m^{-3}), significantly less than the density of water, but lipids used to increase buoyancy have lower densities than this: around 860 kg m^{-3}. Even so, to achieve neutral buoyancy, enormous deposits of these substances need to be synthesised (or consumed in prey species); and more needs to be added as the animal grows.

Do you think that the lift provided by accumulations of lipids will be affected by the depth of the fish in the water column, in the same way that lift from gas-filled swimbladders can be?

No, because unlike gas, lipids are relatively incompressible, so their volume (and hence their density) is not markedly affected by pressure.

The basking shark and the whale shark, plankton feeders which cruise slowly along with their mouths open ('Seasonal Seas', sequence 3), are both close to neutral buoyancy as a result of huge stores of lipids (fat) in their livers. Many deep-sea sharks can also be neutrally buoyant for the same reason – their livers can occupy 30% of the volume of their bodies and cause them to look quite corpulent.

However, the great majority of elasmobranchs do not store enough lipids to achieve neutral buoyancy. For dogfish and some sharks that spend a considerable proportion of their time resting on the bottom, being neutrally buoyant is not as important as for most other fish. However, all sharks and dogfish benefit from extra lift generated by their asymmetric tails (Figure 6.6). As well as moving from side to side, the tail twists, and generates a net upward force; you will learn more about this in 'Wild Moves: Water', which you will see shortly.

Lift generated by relative motion between the water and an animal's body is known as dynamic lift to distinguish it from lift resulting from buoyancy, which is known as static lift. The commonest type of dynamic lift is generated by the flow of water over pectoral fins. If you study the extended pectoral fins of active fish such as tuna and mackerel, you will see that they are inclined to the horizontal, with the leading edge higher than the trailing edge. This, combined with the 'hydrofoil' shape of the fins, leads to a variation in pressure over the upper and lower surfaces of the fins which results in a net upwards force. As discussed in 'Wild Moves: Water', it was thought that sharks also used their pectoral fins to generate lift in this way, but it now seems that (at least at normal swimming speeds) the lift provided by the tail is more important. This lift force acts upwards at the tail end of the shark and, on its own, would tend to tilt the shark's body downwards. To counter this, the shark swims with its body at an angle.

Mackerel – which as mentioned above, *do* generate lift using their pectoral fins – also swim with their bodies at an angle to avoid sinking when swimming at low speeds. When the body is tilted, the thrust from the tail, which acts along the body of the fish, also has an upwards component. In other words, the tilted body of the swimming mackerel itself generates lift.

If a mackerel was swimming very fast, would you expect its body to be tilted more than usual or less than usual?

It would be tilted less than usual.

Like drag forces, lift forces increase with the square of the speed, and are very small when the swimming speed is small. Because of this, there is a minimum swimming

speed below which a shark or tuna would begin to sink. Large and active swimmers like sharks and tuna already expend a considerable amount of energy in swimming, so the small amount of extra energy involved in swimming to avoid sinking is negligible. The same is true of mackerel.

- Can you suggest why it is important for the plankton-feeding basking shark and whale shark to be neutrally buoyant, i.e. be able to avoid sinking without the help of lift generated by fins or tail?
- Collecting and sieving plankton can only be done efficiently by swimming relatively slowly (in these cases, at speeds of about 1 metre per second, 1 m s^{-1}). This is too slow for the flow of water over the pectoral fins or tail to generate much dynamic lift.

Figure 6.8 shows the approximate distribution of fish with and without swimbladders at different depths in the ocean. As you can see, there is not really a clear-cut distribution pattern of fish with swimbladders and without. Some of the reasons for this probably relate to the issues we have been discussing. Another reason might be that over millions of years, certain fish groups may have changed the depth ranges at which they live, and some which lost their swimbladders on moving down into the deep sea subsequently moved back up into mid-depths.

The compressibility of gas means that with increasing depth in the ocean, gas-filled swimbladders become increasingly inefficient. Furthermore, with increasing pressure, gas becomes more soluble, so producing gas for the swimbladder, and retaining it there, becomes more expensive in terms of energy. Therefore, the swimbladders of many mid-water and deep-sea fish contain not gas, but lipids. Many deep-sea fish with swimbladders cruise slowly just above the sea-bed, and use their swimbladders to detect low frequency (low pitch) sound.

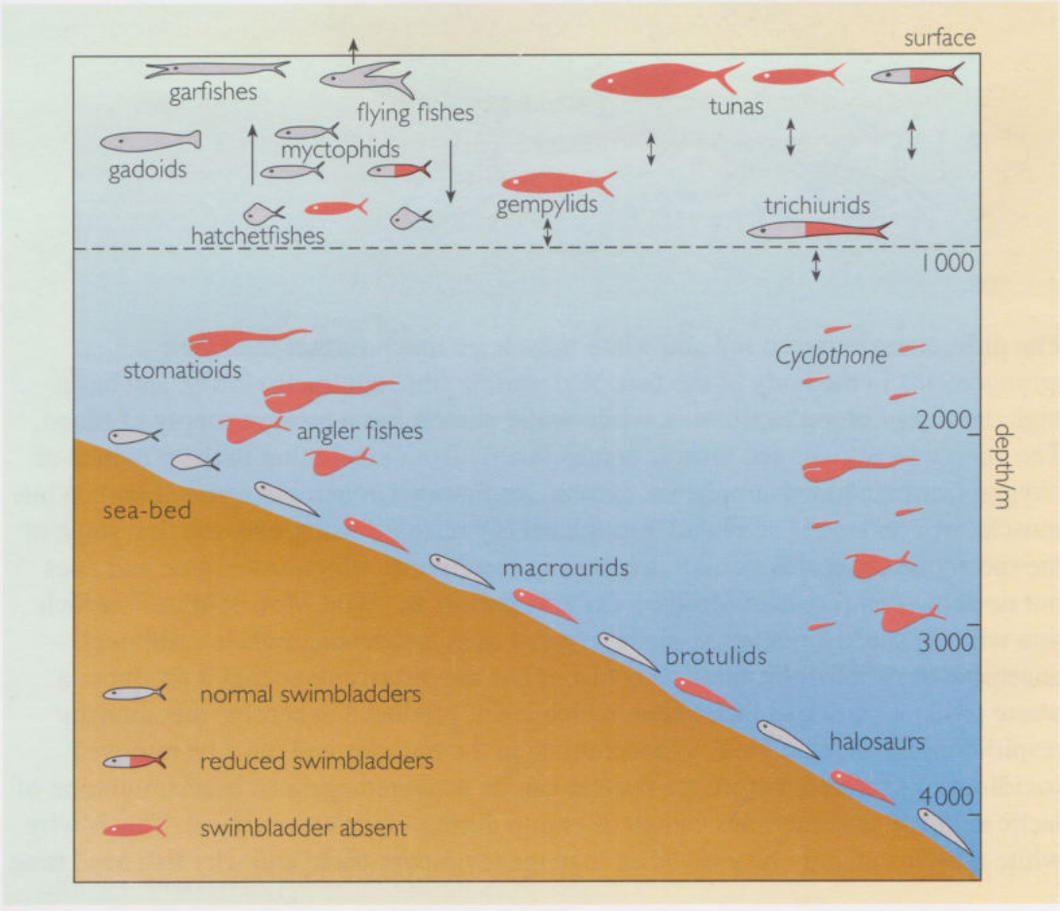


Figure 6.8 Diagram to show the distribution of fish with and without swimbladders at different depths in the ocean (see key). You should imagine the sea-bed to continue up to the left into shallow water. (The dashed line indicates the bottom of the twilight zone; it does *not* indicate a sharp cut-off in the distribution of fish with swimbladders, as some mid-depth fish *do* have swimbladders. Vertical arrows indicate groups that undergo vertical migrations, a topic that will be covered in Chapter 9.)
Do not worry about not knowing some of the fish names; myctophids are lanternfish; *Cyclothone* is also a luminescent fish; gadoids are the group that includes cod, saithe and haddock; trichiurids are scabbardfish; macrourids are rat-tails (which appear in 'The Deep'); halosaurs are deep-sea eel-like fish; brotulids live in the very deepest regions, including ocean trenches.

There are also some good reasons for bottom-living fish *not* to have a swimbladder.

What advantages might there be for flatfish like plaice (*Pleuronectes platessa*), that normally rest on the bottom, not to have a swimbladder?

Fish that normally rest on the bottom need to be able to resist being swept along by bottom currents, and often need to be able to settle into the bottom sediment to hide. For both of these reasons, it would be advantageous to be denser than water.

6.4 Swimming muscles

As mentioned at the start of Section 6.2, most of the muscle of fish is white muscle which, in fish living in the upper 500 m of the ocean, is used only in fast 'bursts' of swimming. For normal cruising – that is, highly efficient steady swimming, the equivalent of jogging – these fish use a thin layer of red or brown muscle which is usually situated along the flanks close to the skin. Figure 6.9 shows how individual white and red muscle fibres (within the muscle segments) are arranged in a typical teleost fish. Note the helical arrangement of the white muscle fibres, which are arranged rather like the twisted fibres of a rope. This helical arrangement effectively multiplies the effect of a muscle contraction by about four, i.e. it causes the body to curve much more than a similar contraction of the red fibres along the flank. The white muscle thus allows swimming in 'low gear' compared with the 'high-gear' swimming ('cruising') attained using red muscle. (Note, however, that for reasons which will become clear in Chapter 10, most deep-sea fish have *no* red muscle.)

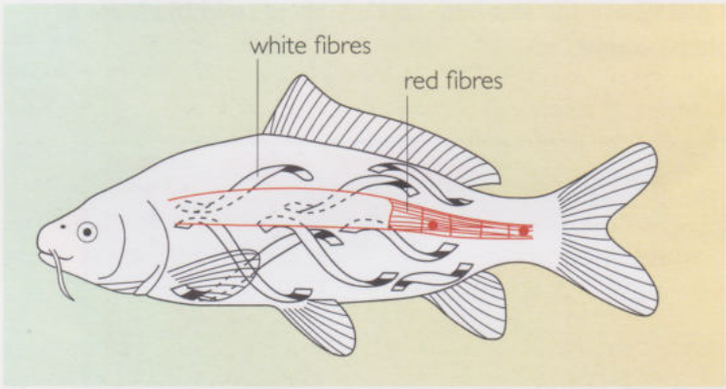


Figure 6.9 Arrangement of superficial red muscle fibres and deeper white muscle fibres (within overlapping muscle segments). The white muscle fibres account for about two-thirds of all the muscle.

The differences between red and white muscle go much further than their arrangements in the body of the fish. Red muscle fibre contracts slowly, and has a high density of blood capillaries, while white muscle has a meagre supply of blood. The energy to activate red muscle comes mainly from respiration in the presence of oxygen from the blood supply, i.e. aerobic respiration (or aerobic metabolism). White muscle, by contrast, is activated through energy released using only the first stage of the metabolic processes usually involved in respiration, which saves time and does not need oxygen (i.e. is *an*aerobic). For this reason, in 'Wild Moves: Water', which you will see shortly, white muscle is referred to as 'anaerobic muscle'. Although anaerobic metabolism/respiration is fast, it has the disadvantage that it produces a waste product known as lactic acid, which is not produced in aerobic metabolism/respiration. Lactic acid tends to accumulate in the muscles and must be removed (oxidised or excreted) before the muscle can be activated again (it is accumulation of lactic acid which sometimes causes us cramp during vigorous exercise). This is why white muscle can only be used as an 'emergency power pack' and why fish need time

to recover after white muscle has been used (as you will see in 'Swimming in Fish: an experimental approach' and 'Wild Moves: Water'). (Don't worry if you did not fully understand this discussion of red and white muscle. It was provided as background to some of the DVD sequences.)

6.4.1 Warm-bodied fish

As 'Open Ocean' showed, tuna are fast and tireless swimmers. They do not undertake 'burst' swimming, but maintain high speeds for long periods of time – more like a middle-distance runner than a sprinter. They are able to maintain higher swimming speeds than most other teleosts, and for much longer.

Question 6.4 On the basis of what you have read so far in this chapter, list at least three adaptations of the tuna that help it to swim fast and efficiently. ◀

Rapid swimming in large fish is very expensive in metabolic terms – most large fish can only keep up high-speed swimming for a few minutes. In the case of some of the larger tunas (and certain species of shark), part of the explanation for their spectacular swimming performance probably lies in the fact that – unlike other fish, which are cold-bodied – they can maintain the temperature of their muscles significantly above the temperature of the water in which they are swimming. The muscles of bluefin and skipjack tuna, for example, are both normally 5–10 °C above the water temperature. This seems to allow the metabolic rate of tunas to approach that of mammals (cf. Section 2.1.2), so allowing sustained swimming.

These relatively high muscle temperatures are achieved by an arrangement of blood vessels that reduces heat loss to the environment from certain areas of the body. In most fish, the blood is delivered through main vessels that lie just beneath the spinal column, with branches delivering the blood to the outer parts of the body. Tunas, by contrast, have their blood vessels just below the skin, with smaller vessels delivering blood into the interior. This allows heat generated within the body to be conserved. In tunas, the heat generated by the red muscle is also conserved because it is positioned either side of the spinal column, an arrangement which again differs from that in most other fish (Figure 6.10), where the red muscle is along the flanks. (This central position of the red muscle in tunas could also help explain their efficient 'stiff-bodied' swimming.)

In most fish, body heat is lost to the surrounding seawater from the blood passing through the gills (where oxygen is taken up from the water). Tunas have an arrangement

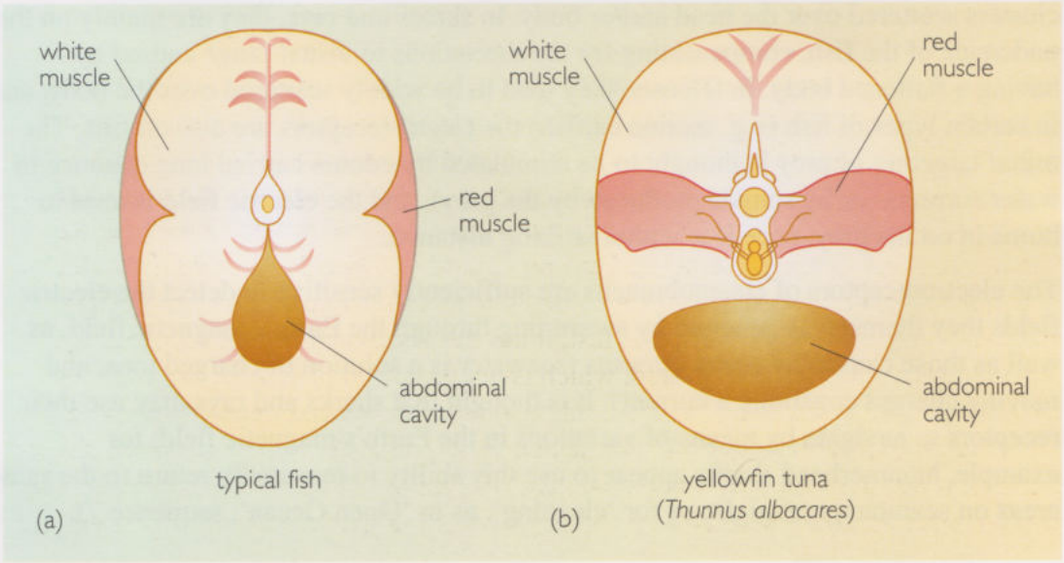


Figure 6.10 (a) Idealised cross-section of a typical fish body showing the large mass of white muscle and the mainly superficial layers of red muscle. (b) Idealised cross-section of the body of a yellowfin tuna, showing the distinctive distribution of red muscle on either side of the spinal column.

of blood vessels that greatly reduces this heat loss from the gills. Throughout the whole body there is a series of arteries where the blood flow is in the opposite direction to the flow in veins lying close to them. This 'countercurrent heat exchanger' ensures that most of the heat produced in the muscles and warming the blood in the veins, is passed directly into the adjacent arteries. It therefore does not get carried to the gills, and instead is trapped in the tuna's body.

6.5 Feeling and hearing

As noted in Section 2.1.1, for an animal living immersed in water, the difference between feeling and hearing is rather blurred, and the receptors that most aquatic animals use to hear (i.e. receive sound waves; cf. Figure 2.2) are very similar to those that they use to detect water motion. These receptors are situated on or near the outer surface of the body (sometimes connected to internal structures such as earbones), and may be bristles or hairs, or in the case of fish, sensitive hair cells, carried in structures known as 'neuromasts'. Thousands of neuromasts, each carrying large numbers of hair cells, are embedded in the membrane lining the ear, and are also situated on the surface of the skin (in the case of fish larvae), or (more usually) enclosed in grooves or canals, which form a *lateral line* system. This consists of one or more neuromast-bearing canals running the length of the body along each flank, which may or may not join up with a group of canals on the head. All these canals connect to the surrounding water via a series of pores or small tubes. Fish of the herring family do not have lateral lines along their bodies, but have very elaborate head canals which are effectively open to the surrounding water.

A surprising number of fish in different groups possess *electroreceptors* – sense organs that can detect electric and electromagnetic fields. Living animals generate small electric fields, and in certain fish the electroreceptors are so sensitive that they can detect the small steady electric fields associated with living prey hiding within the sea-bed sediment.

Question 6.5

Thinking back to 'Tidal Seas', can you recall any examples of fish which hunt using electroreception? To which taxonomic class do these fish belong? ◀

All elasmobranchs, and some teleosts, have organs which can detect electric fields. These are derived from neuromasts (mentioned above), and in elasmobranchs are in clusters scattered over the head and/or body. In skates and rays, they are mainly on the underside of the fish, compensating for the limitations to visual range caused by having a flattened body. In teleosts, they tend to be widely scattered over the body, and in certain types of fish (e.g. marine catfish) the electroreceptors are also on fins. The initial targeting of prey is thought to be stimulated by odours carried long distance in water currents (or by sounds produced by the prey), and the electric field is used to home in on the prey, once it is within striking distance.

The electroreceptors of elasmobranchs are sufficiently sensitive to detect the electric fields they themselves generate by swimming through the Earth's magnetic field, as well as those caused by ocean currents (seawater is a solution of charged ions, and moving charges constitute a current). It is thought that sharks and rays may use their receptors to navigate by means of variations in the Earth's magnetic field; for example, hammerhead sharks appear to use this ability to repeatedly return to the same areas on seamounts (at night, or for 'cleaning', as in 'Open Ocean', sequence 7).

Many fish which possess electroreceptors also have organs which can *generate* electric currents. These organs are nearly always derived from modified muscle fibres. In the case of the electric ray, *Torpedo* (and the 'electric eel', found in freshwater), the electric discharges are sufficiently powerful to stun prey, or to act as an effective defence. It seems that for many fish, the weak electric fields they generate are useful because their electroreceptors can detect distortions of the field resulting from the presence of other animals. All skates have electric organs along their tails. These produce weak intermittent discharges which become more frequent when two individuals meet, and are probably used for communication.

6.6 Schooling

Unfortunately in this short course, it is only possible to touch on a few of the more interesting aspects of fish behaviour and physiology which relate to the Blue Planet programmes. However, there is one type of behaviour that we cannot ignore, not least because it is very obvious in a number of sequences – this is *schooling*. Schooling is the intentional massing together of large numbers of fish (or squid), rather than the crowding that may occur as a result of many animals being attracted to (say) a particularly good feeding area, or being pushed together by current patterns (as occurs, to some extent, in the case of the sardines off the coast of Natal).

Although feeding schools may consist of more than one species, schools of actively swimming fish are nearly always of one species only. The 'bait balls' of small fish that appear in the Blue Planet programmes (e.g. the anchoveta in 'Open Ocean' (end of sequence 7)) appear to have formed as a defence against predation.

How might the formation of a tight 'bait ball' reduce predation?

As suggested by the narration, the fish in the centre of a tight 'bait ball' are (relatively) protected. Those on the outside of the school are most vulnerable to predators (each fish spends a fairly brief time on the outside) and those individuals that become isolated are picked off first.

It is also possible that schooling is intended to confuse predators. Schooling fish may swim towards predators or even form rings around them, presumably to make it difficult for them to concentrate on any particular fish. Tightly schooling fish usually have silvery sides and (as in the case of the anchoveta) may swim so as to produce a wave-like effect on the outside of the school, and this may further confuse predators.

As suggested in 'Wild Moves: Water', schooling may also allow swimming to be more efficient, because in a school, each fish swims in the 'slipstream' of the fish in front. In other words, it makes use of vortices produced by the fish ahead (cf. Figure 6.2), rather in the way that birds flying in a 'vee'-formation use vortices shed by the wings of the bird in front.

But how do schooling fish manage to swim in such perfect co-ordination? The answer may lie in the highly sensitive hair cells in the lateral line head canals, which during schooling are continually receiving information about the movement of the fish directly ahead via the water movements that they generate.

▶▶ This is a good time to watch the two programmes about how fish swim, on DVD 2. We recommend that you read the 'General notes' and the 'Activities' paragraphs, and then play both programmes all the way through. You can then read the notes relating to individual sequences and, if you wish, play the programmes, or individual sequences, again. ◀◀

Notes on 'Swimming in Fish' and 'Wild Moves: Water'

General note The first of these programmes was made some time ago, but all the principles described in it remain valid. 'Wild Moves: Water' briefly revisits the topics covered in detail in 'Swimming in Fish: an experimental approach', and revises much of what you have read in this chapter. It also looks at the results of some recent research which casts light on how dolphins manage to swim so much faster than their muscles should in theory allow, and includes footage which reveals some of the deep-diving techniques of marine mammals.

Activities While watching these programmes, jot down some notes to help you answer the questions which follow.

'Swimming in Fish'

Sequence 1 The word for blocks of muscle is spelt 'myotomes'.

Sequence 4 At the very end, the narration says: 'Certainly, more sophisticated transmitters will be one major avenue of advance, so that fish can be studied in the best possible environment – their own.' Such transmitters ('smart tags') have now been developed and transmit information relating not only to the fish's physiology, but also to the surrounding environment.

'Wild Moves: Water'

Sequence 8 This sequence may remind you of the discussion on 'Moving through seawater' and Figure 2.3 (Section 2.1.2).

Sequence 9 The 'baby shark' is in fact a dogfish. The vortices spinning off its tail (made visible by the reflective particles and represented in colour on the computer screen) are equivalent to the vortices shown in Figure 6.2b, but are different because of the asymmetric tail of the dogfish and the way the tail moves.

Question 6.6 relates to 'Swimming in Fish', Questions 6.7 and 6.8 relate to both programmes, and Question 6.9 relates to 'Wild Moves: Water'.

Question 6.6 For each of the two statements below, say whether it is true or false, and why.

'As swimming fish increase their speed, there is a definite point where white muscle takes over from red muscle.'

'White muscle is particularly useful for out-swimming predators because it can be used for sustained periods.' ◀

Question 6.7 What fundamental (potentially problematic) aspect of their bodies affects the swimming styles of both mackerel and sharks? Do mackerel and sharks use the same techniques to combat this potential problem? (For the purposes of this question, ignore the special case of basking sharks and whale sharks.) ◀

Question 6.8 Why don't marine mammals need buoyancy aids, like swimbladders or accumulation of low-density fats? ◀

Question 6.9 Dolphins swim much faster than their muscles should (in theory) allow. Briefly outline *at least three* possible contributory reasons for this. ◀

▶▶ If you have the time, you might like to watch 'Open Ocean' again, bearing in mind what you have learnt in Chapter 6. ◀◀

Coral reefs

7

In Chapter 4 and 'Seasonal Seas', you saw that temperate seas teem with life every spring because surface waters have been 'restocked' with nutrients mixed up from below during the winter storms. The corollary of this is that, except in areas of upwelling, tropical waters, which are rarely turned over by storms, are mostly very poor in nutrients. They therefore support very low primary productivity and hence low productivity generally, despite the fact that they receive high levels of sunlight all year round.

So this invites the following question: how is it possible for coral reefs, found only in tropical waters, to be almost bursting with life, supporting not only a wide variety of species but also extremely large numbers of individuals?

The answer is that coral reef ecosystems conserve and recycle nutrients very efficiently. Before we go into how this achieved, we should explain what coral reefs are.

7.1 What is a coral?

Although coral *reefs* are found only in the tropics, corals themselves are very widespread organisms. Solitary corals (i.e. those which do not form colonies) are found in shallow waters (e.g. around the British Isles) and large solitary species are also found on reefs. There are also deep-water corals which form mound-like colonies*; these may be extensive but are distinct from the type of reef that grows in tropical waters.

- Thinking back to Section 1.1 and particularly Figure 1.4, would you say corals are ancient animals, or did they evolve relatively recently?
- Corals belong to the Phylum Cnidaria, and are very ancient animals (group 1 on Figure 1.4).

An individual coral animal, known as a polyp, looks very like a sea-anemone, and consists of a tubular body with a central mouth surrounded by a crown of tentacles (Figure 7.1). The fact that corals are tubular (and so radially symmetric) tells us that the first corals existed before the Cambrian 'explosion' in diversity. They were probably anemone-type animals which did not produce calcium carbonate skeletons.

So, modern reef-building corals are effectively colonial sea-anemones that secrete supports (skeletons) of calcium carbonate (i.e. limestone) into which they can withdraw for protection. As you may remember from the Notes on 'Seasonal Seas', corals and sea-anemones belong to the Class Anthozoa, the 'flower animals'. A living coral colony forms a thin layer over a limestone foundation which has been almost entirely produced by previous generations, and may be thousands of years old.

Each coral polyp sits in a cup-like depression in the skeleton, which has ridges or plates radiating from the centre. This ridged cup is known as a calyx. Depending on the species and the time of day, the polyp will be extended out of the calyx to varying degrees, and at times of danger or physical stress it contracts down into the bottom of

* You may have seen news reports about possible threats to such 'reefs' growing along the continental slope to the north and west of the UK, from deep-water oil exploration and exploitation. There will be more about deep-water corals in Chapter 11.

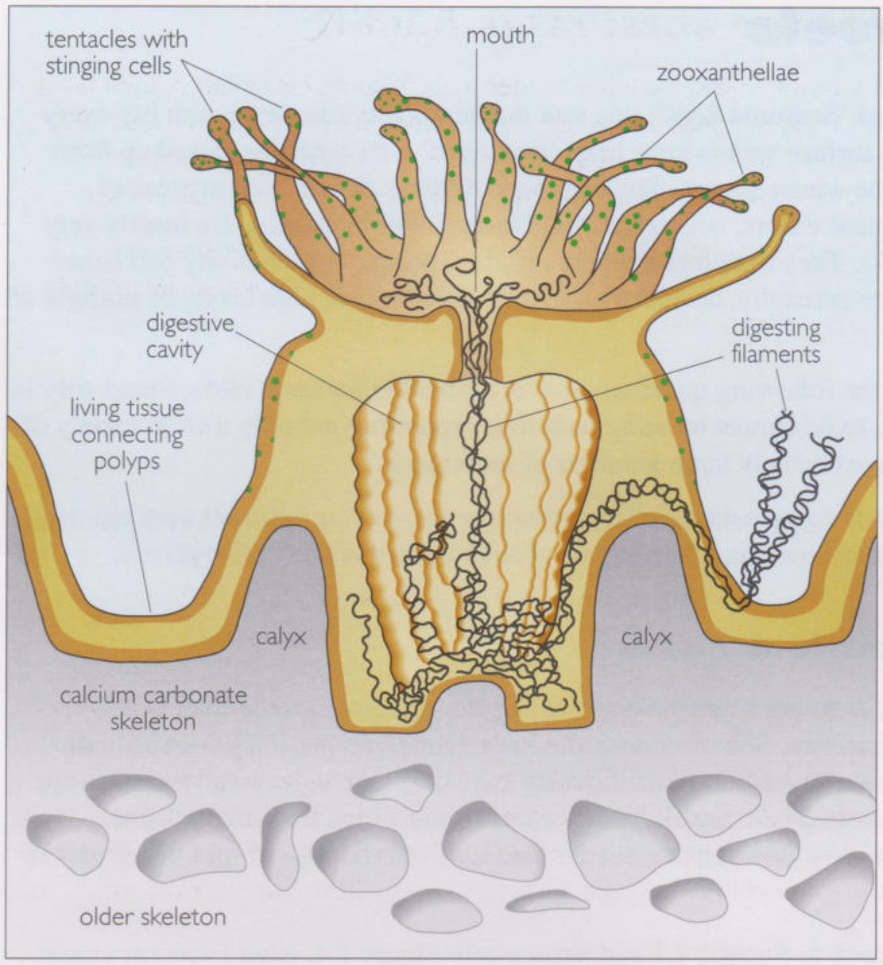


Figure 7.1 Schematic diagram of a coral polyp. An individual coral polyp is typically about 0.5–1 cm across The digestive filaments are the white filaments seen in 'Coral Seas' (sequence 4). The green dots represent zooxanthellae (see text). When the corals contract, the soft tissue is pulled down into the narrow slots between the 'ribs' of the calyx.

the calyx. As you will see in 'Coral Seas', most reef coral species feed at night. They capture zooplankton with their tentacles which have stinging cells ('nematocysts') and carry them to their mouth and central gut, which is folded into pleats that fit between and around the plates of the calyx (there is an animation showing this in 'Coral Seas', sequence 3).

Reef-building coral colonies can be divided into massive and branching forms. Massive corals tend to be mound-shaped and somewhat irregular, while branching corals may look like tree branches or have a more-flattened shape like elk horns. Massive corals tend to grow slowly, no more than about 1 cm per year in any direction. Branching corals grow much faster, of the order of 10–15 cm per year. You can see time-lapse footage of a growing branching coral at the beginning of 'Coral Seas'.

The shape of the colony is to a large extent determined by where the new 'buds' form and the degree of separation of the resultant polyps. An extreme example is provided by the massive 'brain corals' (*Meandria*), where the polyps grow side by side but do not separate, resulting in rows of mouths fringed by rows of tentacles. It is the intersection of rows of polyps and tentacles that produces the pattern which looks like a human brain. In branching corals, the new polyps form at or towards the top of an existing polyp.

Budding is a form of asexual reproduction, and produces identical individuals or clones. As you will see in 'Coral Seas' (sequence 11), corals also reproduce by sexual reproduction, i.e. by producing eggs and sperm. The resulting coral larvae then drift as members of the plankton until they find suitable substrates on which to develop into new coral animals.

7.2 Where are coral reefs found?

Reef-building corals can only live where water temperatures never fall below about 18 °C, and grow best at temperatures of 25–29 °C. They do not thrive in water with low or variable salinity and cannot tolerate low light levels or turbid water. Reef-building corals are therefore found in shallow, clear, warm waters in the tropics.

They are widespread throughout the tropical Indian Ocean, in the western tropical Pacific, in the Caribbean and along the coast of southern Brazil, but are found only in restricted areas in the eastern Pacific and the eastern Atlantic.

Question 7.1 By reference to Figure 5.2, can you explain why conditions on the western sides of the Atlantic and the Pacific are more conducive to coral-reef growth than conditions on the eastern side? ◀

We mentioned above that reef-building corals only grow in clear shallow water, and it might have occurred to you that these are conditions which favour plant growth. At first sight, this could seem strange because corals are animals. In fact, they grow only in well-lit waters because (as you will see in 'Coral Seas') they have a symbiotic – i.e. mutually beneficial – relationship with single-celled algae that live within their tissues. These algae, known as *zooxanthellae* (pronounced 'zoo-zanthelleye'), are a special form of a particular species of dinoflagellate (Section 1.3). Dinoflagellates living in the water column can 'swim' using two whip-like structures known as flagellae, and coral algae removed (or ejected) from a coral change to this swimming form. It seems that although all zooxanthellae are the same species of dinoflagellate (*Symbiodinium microadriaticum*), each species of coral 'host' has its 'own' strain of this species.

Coral seems to benefit from the presence of the algae in two main ways. Like planktonic algae, the zooxanthellae use carbon dioxide and water to manufacture carbohydrate, to which the coral also has access. This 'free' carbohydrate makes up more than 90% of the coral's nutritional needs. Photosynthesis by the zooxanthellae also increases the rate at which the corals can produce their calcium carbonate skeleton (although exactly how this works is not clear). In their turn, the zooxanthellae benefit from the partnership by being protected (to some extent) from grazing by reef animals, and also through access to nutrients excreted by the coral.

Apart from warm, clear shallow water, reef-building corals need a hard substrate on which to establish themselves in the first place. There are three basic types of reef: fringing reefs, barrier reefs and atolls. Fringing reefs develop in shallow water along the shore, and thrive best in arid regions, where river outflow and freshwater run-off are limited. They are usually less massive than barrier reefs and atolls, and are generally patchy because they are easily damaged by sediments (in river outflows or stirred up by storms) and by human activities.

Barrier reefs and atolls are found in areas where the sea-level locally has been rising and/or the sea-bed has been sinking. Since the end of the last glacial period about 11 000 years ago, melting of the ice-caps has meant that sea-level has been rising world-wide. At the same time, movements of the Earth's crust, either upwards or downwards, have meant that locally, sea-level may have gone down as well as up. Barrier reefs (where there is a lagoon between the coast and the reef) and atolls (which encircle a lagoon) start life as fringing reefs, along mainland coastlines (in the case of barrier reefs) or around islands (in the case of atolls). Corals grow best within about 10–20 m of the sea-surface and active reef-building ceases below

25–50 m (cf. Figure 4.8). If (as is generally the case) sea-level above the reef is rising, the reef must build upwards to remain in conditions that enable the zooxanthellae to function well. As a result of continued upward growth over perhaps thousands of years, barrier reefs can be many tens of metres thick.

Many reefs have characteristics of fringing reefs and barrier reefs. Fringing reefs may grow to great thicknesses if the coastal margin is subsiding. In this case, there is a 'reef flat' between the coast and the reef crest (the highest and most vigorously growing part of the reef), rather than a lagoon as in the case of a barrier reef. There are also reefs described as 'platform reefs', which are complexes of corals found on continental shelves and shallow platforms like the Bahama Bank. The Great Barrier Reef off the eastern coast of Australia is not a barrier reef of the type described above, but is an enormous aggregation of reefs of different types, shapes and sizes.

Atolls develop from reefs that have built up around volcanic islands (most of which are no longer active volcanoes). Some are millions of years old.

By reference to Chapter 2, especially Figures 2.4 to 2.7, can you suggest why volcanic islands might have a tendency to subside over the course of millions of years?

As ocean crust moves away from the spreading ridge where it originally formed, it cools, becomes more dense, and subsides (Figure 2.6). As a result, volcanic islands that rest upon that crust also subside, and many eventually become seamounts.

The edifices of coral that have grown up around the seamounts over thousands to millions of years may be hundreds to thousands of metres thick. Many are now substantial islands, with terrestrial vegetation and human populations. As Figure 2.5 shows, the western Pacific Ocean has a very large number of volcanic islands, which is another reason why it has many more coral reefs than the eastern Pacific.

Apart from the isolated mid-ocean islands and seamounts, what other volcanic features are common in the western Pacific?

The western side of the Pacific is characterised by island arcs, which erupted on the landward side of subduction zones (Figures 2.5 and 2.6).

Figure 2.5 shows that the Caribbean also has a number of island arcs. The corals you will see in 'Coral Seas' were filmed in a wide variety of locations – including the Caribbean, the Red Sea and the Great Barrier Reef – and on different types of reefs.

7.3 The reef community

In 'Seasonal Seas', you saw how a kelp forest supports a distinct community of organisms, often living in intimate association with the kelp plants. A coral reef community is similar, in that the habitat is provided by living members of the ecosystem itself – mainly the corals. However, much of the physical structure of a coral reef is also provided by other reef inhabitants. For example, there may be mounds of bivalves, and of a type of gastropod whose tubular shells are cemented together by 'coralline algae'. Coralline algae are so called because, to deter grazers, they secrete calcium carbonate, and this means that they make a rock-like substrate. These algae, which are very often red, have both branching forms and encrusting

forms (Figure 7.2). Indeed, as corals themselves do not thrive if battered by waves, the topmost part of the reef tends to be dominated by coralline algae. As well as cementing themselves to the reef surface, these algae also cement to the reef chunks of coral broken off by waves, building up what is known as an 'algal ridge'. Below the surface of the algal ridge is a labyrinth of tunnels and cavities which harbour many types of small molluscs and crustaceans.

Like the coral-reef habitat, the sea-bed sediment on and around the reef is provided by the organisms themselves. In 'Coral Seas' sequence 4, we see parrotfish adding to the coral sand, but they are not alone – sponges living within the carbonate skeleton break it down, and coralline algae, molluscs, sea-urchins and many other organisms contain calcareous components that are added to the sand when they die.

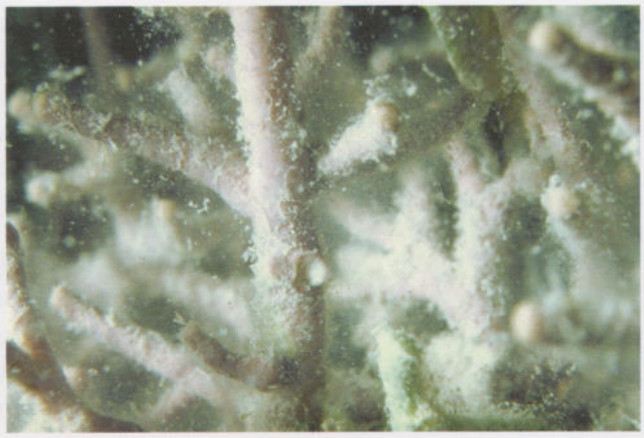


Figure 7.2 Close-up of a carbonate-precipitating 'coralline' alga. This is a specimen of the red alga *Goniolithon*, whose branches are encrusted with other carbonate-precipitating organisms.

7.3.1 A riot of colour – but no green!

Although coral reefs are so colourful, corals themselves have subdued hues of brown, green or blue imparted by the zooxanthellae. The bright colours are provided by the other members of the reef community – especially sponges, anemones, gorgonians (sea-fans) and fish, but also molluscs, crustaceans, echinoderms (e.g. starfish and sea-urchins) and polychaete worms.

But given that phytoplankton are not abundant in these nutrient-poor waters, where are the green plants – the primary producers – supporting this ecosystem?

- Can you suggest one or more reasons for the lack of visible plants?
- One reason is that some of the reef algae – the zooxanthellae – are hidden in the corals. Another reason is that coralline algae, which make up a significant proportion of the plants on the reef, are not green and so do not look like plants (Figure 7.2).

Yet another reason for the apparent lack of primary producers is that the filamentous green algae that do grow on the hard surfaces of the reef are grazed down by herbivores (particularly fish) at such a rate that the amount present at any one time (the 'standing stock') is small – this is clear from several sequences in 'Coral Seas'. It has been shown that if grazers are excluded from part of a reef, it quickly turns green.

However, we have still not explained how reefs can have such enormous productivity, given that they are found in the nutrient-poor waters of the tropics. Part of the reason is that the zooxanthellae–coral partnership is very efficient, and so most of the nutrients that the algae need are supplied by the coral polyp. Indeed, corals are not the only reef animals to have symbiotic relationships with zooxanthellae – there are many others, including soft corals, colonial anemones, and the giant clam. It is also advantageous to the system as a whole that corals can obtain food by capturing zooplankton (they cannot digest phytoplankton); they can also absorb organic substances directly from the surrounding water, as well as collecting food particles by means of mucus threads (which are also used to clear sediment particles away).

Furthermore, the structures of reefs themselves, particularly atolls, tend to trap nutrients. On death, the reef fauna decompose within the reef system, and the nutrients released by this decomposition can be taken up by the zooxanthellae and other reef algae, rather than being carried away to be used by phytoplankton elsewhere.

As 'Coral Seas' makes clear, every square centimetre of the convoluted surface of the reef structure, and every nook and cranny within the reef, provides living space for some type of organism. In the crowded reef environment, there is a great deal of interaction between organisms – symbiotic, predatory, reproductive, social and competitive. There is not space to discuss such interactions at length here, but the programme shows some fascinating examples, both cooperative and competitive.

Corals themselves are continually in competition with one another, both for light and for space. Because they grow faster, branching corals tend to overshadow slower-growing forms, preventing them from flourishing, with the result that there may be patches consisting only of branching corals. However, slow-growing massive corals have a way of retaliating, as explained below.

In sequence 4 of 'Coral Seas', you will see a coral of one species digesting its neighbour, of another species. The polyps of the 'aggressor' coral extrude filaments of their gut through their mouths and through temporary openings in their walls, and literally digest the soft tissue of the neighbouring coral, exposing the skeletons beneath. It seems that there is a coral 'pecking order', in that each coral species only attacks certain other species, and is itself only attacked by certain other different species. Corals of a species that is intermediate in the aggression pecking order may be consuming their neighbours on one side, while themselves being consumed by neighbours of a different species on the other side!

▶▶ You should now watch 'Coral Seas' on DVD 3. We recommend that you read the 'General notes', and then play the programme all the way through. You can then read the notes relating to individual sequences and play the programme again or, if you wish, replay individual sequences. There are quite a few activities associated with this programme, so you should tackle these whenever suits you best. ◀◀

Notes on 'Coral Seas'

General note Most of this programme was filmed during daylight, when the coral polyps were withdrawn into their calyces, so the radiating ridges of the calyces are clearly visible.

Activities While watching, make a note of the different ways in which colour and patterns may be used (this will be followed up in Question 7.6). Also, make a note of any echinoderms that you spot. If you need to be reminded about echinoderms, look back to Section 1.2, particularly Figure 1.7.

Sequence 11 shows the reproductive behaviour of (1) surgeonfish, (2) banded pipefish, and (3) corals. Make brief notes about the strategies used by each of these animals to maximise the number of offspring.

Also, to apply some of the ideas introduced in Chapter 6, try the following exercises, which are followed up in Questions 7.2 to 7.4:

- When you get to the butterflyfish (towards the end of sequence 3), use 'pause' and sketch the overall shape of the butterflyfish and the shape of its tail.
- Similarly, sketch the shape of the tails of the parrotfish (sequence 4).
- Sketch (or make notes about) the shape of the jacks (sequence 5).

Sequence 1

- At the beginning, you can see some planktonic animals, including a radiolarian (brown, with spines), a small medusa, a small ctenophore, a copepod, and some 'frilly' planktonic worms. There are also some meroplankton (Section 4.4), including some crustaceans (one of which is a crab; cf. Figure 4.12i) and two molluscs, for one of which a coiled shell is visible (cf. Figure 4.12a). (All these animals are nearly transparent, and you would have to use 'pause' to see them at all clearly.)
- As this branching coral grows, note how the position of the new buds determines the overall shape of the coral.

Sequence 2

- The Christmas tree worm is a polychaete (its bristles are obscured by its tube). Its spiral of tentacles is covered with cilia that filter suspended particles from the water.
- The animal extending feathery appendages from amongst the tentacles of a soft coral is a small crab.
- The small fish which grazes the algae on the turtles' shells is a blenny.

Sequence 3

- When watching the animation, remember that it represents a journey down into a single small polyp and the limestone skeleton beneath. The 'pleats' of the gut can be seen (although in the animation they look hard, rather than like soft tissue). At the edges of the pleats are cells producing digestive enzymes, and at the bottom of each pleat the gut becomes highly convoluted, forming the filaments that are extruded in 'intra-coral warfare', coming later. (In the animation, these filaments are shown simply as curled protrusions.)
- Referring to the zooxanthellae, the narration states that '98% of the food that the corals consume is produced by the algae'. This is misleading, as the only food that the corals actually *consume* is that captured by the tentacles and trapped on their mucus threads (not seen in the programme). The useful organic compounds produced by the zooxanthellae are absorbed directly into the coral tissue. The 2% of food that the corals *do* consume provides nutrients for the algae. (In Section 7.2, we say that 'more than 90% of the coral's nutritional needs' are provided by the algae – the precise percentage will vary from species to species, and will change with light levels, etc.)
- The light against which corals need to protect themselves (and perhaps more importantly, their algae) is ultraviolet light, which can damage cells and cause mutations. This is a particular threat in clear tropical waters where all solar radiation can penetrate to greater depths. The reason that the pigments show up in ultraviolet light is that they have absorbed the light and so look different from adjacent areas of the polyp. (This sequence was filmed using different filters – the dramatically contrasting colours are not natural.)
- Butterflyfish eat the soft coral tissue (i.e. they do not feed by grazing on algae).
- For completeness, we should mention that many species of soft corals feed by capturing zooplankton and detritus, both by day and by night.

- Towards the end of the night scenes, you can clearly see capture of food by the coral tentacles. Note that the plankton being eaten is zooplankton – the green that you can see is the zooxanthellae showing through the translucent coral tissue.

Sequence 4

- In the part about 'territorial disputes', you can clearly see how the soft tissue of the coral relates to the limestone calyces.
- Look out for the 'tube feet' or suckers of the crown of thorns starfish.
- Note that the guano provides the nutrients – nitrate and phosphate – that plants (in this case, land plants) need.

Sequence 5 Here is a good example of small fish using schooling to try to confuse predators (Section 6.6).

Sequence 6

- Sponges are the most primitive animals of all. They have no nervous system, no gut, and no distinct tissues or organs.
- This worm is recognisable as a polychaete by the bristles down either side – you may recognise the similarity with ragworms, which are also polychaetes. While this polychaete has an apparatus for seizing prey, others have external feathery gills, or feathery extensions for collecting food from the water column.

Sequence 7 The lionfish seems to be using fake 'angelfish' to add to its camouflage.

Sequence 8 Again, look out for the starfish's tube feet or suckers.

Sequence 9 While the powder blue tangs are grazing on the green algae (and later in the sequence), you can also see quite a bit of red coralline algae.

Sequence 10

- Basketstars are by no means alone in coming out to feed at night. Generally, the animals that are active at night are different from those that are active during the day. This is partly because zooplankton from deeper waters migrate to shallower levels and so are more abundant on the reef; filter-feeding therefore becomes more worthwhile. (We will come back to the topic of vertical migration in Chapter 9.)
- The moray eel (and the pipefish larvae in sequence 11) are employing the style of swimming illustrated in Figure 6.1.
- As the marbled ray swims away from the camera, you can see how it propels itself by means of backward-moving waves passing along its enlarged pectoral fins (Section 6.2).
- In the scenes showing white-tip sharks hunting, you can also see how accretions of molluscs (here mussels and other bivalves) form part of the reef structure.

Sequence 11

- As you will probably guess, sea-horses and these pipefish are closely related (male sea-horses also brood their young). Here, you can see the undulating pectoral and (especially) dorsal fins being used for propulsion while conferring great manoeuvrability.

- The relationship between cuttlefish, squid and octopus will be covered later in the text.
- The eerie sound you can hear in the background is a male humpback whale singing to establish his seniority over other males. Whales visit reefs at certain times of year when wind-driven upwelling increases the nutrient content of the water and makes then temporarily more biologically productive.
- The narration says: 'Corals also reproduce sexually …'. This is because reproduction by budding is *a*sexual reproduction.
- The narration says: 'A few days after the Full Moon in late spring when tidal currents are at their weakest …' but as you know from Chapter 3, this is not correct! It should simply say 'about a week after Full Moon'.

Sequence 12

- In the Caribbean, the stormy hurricane season is the end of summer, when the surface of the ocean is at its warmest. (This footage of the storm shows well how waves result in mixing.)
- These spiny lobsters (actually a kind of crayfish) are walking across flats of coral sand.
- As the crayfish travel down from the edge of the reef, you can just about see how the corals near the surface are more massive while those deeper down are more delicate. (The topic is discussed in Section 7.4.)

Question 7.2 While watching 'Coral Seas', you sketched the shape of the butterflyfish's body and the shape of its tail. Where does this shape fall with respect to the 'fish triangle' in Figure 6.3? What advantages do these body and tail shapes confer on the butterflyfish, and why are these particularly useful in a coral reef? ◀

Question 7.3 How is the shape of the parrotfish tail classified, according to Figure 6.6? How does the parrotfish appear to be swimming? ◀

Question 7.4 What features of the jack (sequence 5) allow it to be one of the key predators on the reef? ◀

Now try Question 7.5, which will revise your understanding of tidal cycles (Section 3.1).

Question 7.5 Why might it be advantageous to corals to spawn together? And can you suggest why mass spawnings occur at night and about a week after Full Moon? ◀

7.3.2 Fish, cephalopods and echinoderms

In this short course, there is not room to discuss all the organisms that appear in the Blue Planet series. However, 'Coral Seas' highlights some groups of animals that are prominent in the course as a whole, so we will use this opportunity to say a little more about them.

Reef fish

The most striking feature of coral reef fishes is their diversity, although the greatest diversity is developed in relatively few groups – it is estimated that 3000 species of fish live in association with reefs in the Indo-Pacific alone. In addition to those fish that graze the filamentous algae living on the reef – including parrotfish, surgeonfish, damselfish and rabbitfish – there are fish that eat the living coral, or *corallivores*. The corallivores include triggerfish, pufferfish and butterflyfish. As you will have seen in 'Coral Seas', both corallivores and herbivores contribute to the erosion of the reef and augment the supply of coral sand.

Reef fishes and other reef animals tend to be brightly coloured and distinctively patterned, presumably because in the clear waters of the reef, colours and patterns are easily seen, even some distance below the sea-surface.

Question 7.6 To what uses can colours and patterns be put? Make a list of as many functions as you can, especially bearing in mind what you have seen in 'Coral Seas'. ◀

Reef fish have very good vision, upon which they rely heavily for complex social and ecological interactions, as well as for avoiding predators. Amongst reef fish (as in many other animals), it is generally the males that have the bright colours and distinctive patterns.

Would you say that the breeding strategy used by surgeonfish to maximise the number of offspring has more in common with that of banded pipefish, or that of corals?

The breeding strategy used by surgeonfish is closer to that of corals than to that of pipefish. Both surgeonfish and corals undertake mass spawnings, releasing large numbers of eggs and sperm into the water column (cf. Question 7.5). Although a large proportion of eggs will be eaten, some will be fertilised, survive predation and develop into young. Pipefish, by contrast, produce a relatively small number of eggs, which are closely guarded until the young hatch.

You may remember from sequence 11 that some of the spawning corals were female (producing eggs), some were male (producing sperm), and some were both male and female – i.e. hermaphrodite – producing eggs 'pre-wrapped' in sperm. Invertebrate animals that cannot move (or cannot move far) are often hermaphrodite – limpets are a good example. This ensures that there are always suitable breeding partners nearby. By contrast, many territorial reef fish are *sequential* hermaphrodites, beginning as small, drab females and later becoming brightly coloured males. For successful breeding, male reef fish must not only compete with other males to mate with females, but also guard breeding sites and sometimes also guard the fertilised eggs, so it pays to be big, fast and impressive. The most effective way to produce a large number of progeny is therefore to be female when small, and male when bigger, older and more experienced.

Cephalopods

In 'Coral Seas', you saw some brightly coloured cuttlefish and, slightly later on, an octopus. You may also remember a school of colour-changing squid (mating adults and babies) in 'Seasonal Seas'. You will probably not have been surprised

to learn that cuttlefish, squid and octopi are related to one another. Their ability to change colour is often used for camouflage against visual predators. (In part II of 'The Deep', you will see that squid can also produce some spectacular bioluminescence.)

Do you recall what phylum squid, octopi and cuttlefish belong to?

As mentioned in the Notes on 'Seasonal Seas', they are molluscs, i.e. they belong to the Phylum Mollusca.

Squid, octopi and cuttlefish are known as cephalopod molluscs or cephalopods (cephalopod = head–foot).

Cephalopods are the most sophisticated of the invertebrates in terms of their nervous organisation and muscular co-ordination, and the complexity of their behaviour. They have well-developed eyes, with some similarities to those of vertebrates, having iris, retina, cornea etc. They are nearly all predators, seizing prey with their circle of arms (which often have suckers), and carrying it towards their powerfully beaked mouth. While octopi have eight arms, squid have ten, including two long suckered tentacles.

For completeness, we should also mention the pearly *Nautilus*, which (sadly) does not appear in any of the programmes. The *Nautilus* is more primitive, and has changed little over millions of years. It has a spiral chambered shell, swims at several hundred metres depth, and varies its buoyancy by controlling the proportions of gas and fluid in the chambers of its shell. It does not have any suckers, but has over 90 arms.

Cuttlefish live in relatively shallow water, and may dive from the surface down to depths of about 200 m. As mentioned in Chapter 6, when swimming up and down in the water column, they regulate their buoyancy by varying the amount of gas in their cuttlebone (which is enclosed in a membrane).

Squid have a horny translucent structure known as a 'pen', which provides support but does not play a role in buoyancy control. They have evolved to catch their prey using speed, and so have lost all heavy shell-like structures. In terms of speed and manoeuvrability they are nearly the equal of fish. The smallest squid are a few centimetres long, and the largest – the legendary deep-sea squid *Architeuthis* – may be 20 m long, including its outstretched tentacles. *Architeuthis* is the largest of all living invertebrates.

Squid of all sizes are highly adapted for rapid jet propulsion: their bodies are torpedo-shaped (cf. Section 6.2), and most of their weight is in the mantle, the muscular envelope that encloses the gut, heart etc., as well as a cavity into which it can take water. When a squid needs speed, it uses giant nerve fibres to bring about a rapid, synchronous contraction of the mantle, forcing water out of the mantle cavity via a siphon near its head, and propelling it away from the direction in which the siphon is pointing. The siphon is flexible, which is why squid can move forwards (head-first) or backwards (tentacles-first), although backward movements are most efficient. Jetting is also used by octopi and cuttlefish. Forward jetting by an octopus can be seen (fleetingly) during the night-time shark hunt in 'Coral Seas' (sequence 10), and in 'Seasonal Seas' (sequence 9). In sequence 11 of 'Coral Seas', you can see the coral sand behind the male cuttlefish being disturbed by a jet of water.

By reference to 'Coral Seas' (sequences 10 and 11) and 'Seasonal Seas' (sequences 9 and 15), can you identify two other methods which squid and/or cuttlefish and/or octopi use to swim or otherwise move around?

(1) Both squid and cuttlefish may swim by sending ripples along their fins. You can see this technique clearly in the 'squid ballet' in 'Seasonal Seas' (sequence 15), where the squid swim both backward (ripples moving forwards along the fins) and forward (ripples moving backwards). The babies seem to be trying to swim by 'jetting'. In 'Coral Seas' (sequence 11), the male cuttlefish can be seen rippling its 'frill' as it pursues the female.

(2) Octopi and cuttlefish may both 'walk' or 'crawl' along the sea-floor (sequence 9 of 'Seasonal Seas', and start of sequence 10 in 'Coral Seas'; sequence 11 in 'Coral Seas').

For octopi, 'crawling' is probably the most common method of movement, with jet propulsion only being used for escape. Most cuttlefish generally employ jet propulsion and swimming by sending waves along their fins. Certain species of cephalopods swim by *flapping* their fins.

Octopi have no internal rigid structures and so can squeeze through surprisingly small openings. There are two groups of octopus, of which the more common type appears in 'Coral Seas'. It lives on the sea-bed around the coast and in deeper water, can be various colours, and has a muscular body and an ink sac. The other type of octopus, sometimes known as a 'sea-bat', was only discovered in the early 1960s. It lives along the continental slope, and spends much of its time drifting over the sea-bed, with its arms spread so that fine membranes between them form a parachute. It is always red or orange, has fins, and a jelly-like body which provides neutral buoyancy.

Echinoderms

In 'Coral Seas', you also saw several echinoderms – animals in the Phylum Echinodermata (cf. Figure 1.7). As mentioned in Section 1.2, all echinoderms have a spiny skin which encloses an internal skeleton of interlocking calcium carbonate plates and have a five-fold symmetry, which is not always obvious. They have a water-vascular system consisting of a water-filled ring encircling the gut, off which branch subsidiary vessels ('vascular' means relating to vessels/tubes which carry fluids within an organism). These water-filled vessels lead to tube feet – at least 2000 of them – which are controlled using variations in water pressure (i.e. hydraulic pressure) and – as shown in 'Coral Seas'– can be used to 'walk', grip the substrate, and catch or manipulate food.

Which echinoderms did you see in 'Coral Seas'?

The echinoderms that were fairly easy to spot were the crown of thorns starfish (sequence 4) and the orange starfish which was being carried away by the harlequin shrimps (sequence 8); and the basketstar that emerged from a crevice in the coral at nightfall (beginning of sequence 10).

At the start of sequence 4, there is a very brief glimpse of a purple brittlestar – if you spotted this, you were doing very well. (The black animals resembling sea-lilies (stalked crinoids), near the start of sequence 2, are in fact fanworms, i.e. polychaetes.) Strangely, there are no shots of sea-urchins, which are usually the most abundant echinoderms on coral reefs.

It is easy to see that starfish (and brittlestars) have a five-fold symmetry, but in the case of the basketstar this is nowhere near as clear! In these echinoderms, the five arms have branches, and these in turn have smaller branches, which is why the

overall effect is of a mass of coiled tentacles. In the daytime, they tend to hide with the arms wrapped into a compact ball. At night, they spread out their arms and use their tube feet to catch zooplankton. As you may recall from Figure 1.7, other echinoderms include sea-cucumbers and featherstars.

7.4 The influence of wave action on reefs

As discussed in Section 7.3, coral reefs grow up towards the light while being continually eroded by members of the reef community. This erosion weakens the reef structure, with the result that a large storm can wreak havoc. Towards the end of 'Coral Seas', there are some spectacular scenes of storms battering a coral reef, and of crayfish evacuating the reef top and moving down into deeper water. It is quite hard to see, but the crayfish are moving down through different zones, which are found to a greater or lesser extent on most reefs. These zones are analogous to those on a rocky shore but in this case they are determined by the depth *below* the waves.

Seaward of the algal ridge, which is the highest part of the reef, there is a 'buttress zone' where the coral is subjected to extremely vigorous wave action. Usually, wave-cut channels extend down from the top, and sand and coral debris are transported down these channels into deeper water. This is sometimes called a 'spur and groove' formation, and the channels are known as 'surge channels'. Coral growth is limited in the grooves, but many invertebrates and fish feed on the organic debris that is travelling down them. The relatively high ridges are free of sediment, and do support corals.

Would you expect these to be branching corals or massive corals?

Because of the vigorous wave action, these are robust massive corals, like brain coral (Section 7.1).

In this buttress zone, which extends down for a few tens of metres, there are also encrusting corals and algae. Further seaward down the slope, there is a zone of relatively robust branching corals, and then at about 50 m depth there is a change to more delicate corals – including the so-called black corals – which have long slender branches that extend out beyond the shadows cast by other corals. Here are also soft corals and sea-fans, which extend their delicate feathery branches out into the current to capture food particles and plankton. As you might expect, it is not only the coral that shows a vertical zonation – this is also seen in the invertebrate community and the fish that live amongst the coral.

As the depth zonation is largely determined by the intensity of wave action, and most reefs are in regions affected by a prevailing wind direction (often easterly, because of the Trade Winds; Figure 5.1), the precise depths at which the changes occur depend on whether the reefs are exposed to the prevailing winds (i.e. are facing to windward) or are more sheltered (facing to leeward) – of course, atolls have both windward and leeward sides. So, more delicate corals are found at shallower depths on the leeward side of a reef. Interestingly, in the Caribbean (and possibly in other areas too), the change from more robust to more delicate corals is largely a result of the same species of corals changing their shape, being more stumpy at shallower depths, and with more horizontal flat 'leaves' in the lower light levels further down.

7.5 Does coral have a long-term future?

While tropical storms may wreak havoc on coral reefs, the reefs usually recover surprisingly quickly, especially as the most rapidly growing corals are found in areas most frequently affected by such storms. Even if a reef is completely devastated by a storm, it is rarely killed completely, because fragments survive and regenerate. The real threats to coral reefs are human activity and climate change.

A common cause of coral mortality is high sediment loads in the water, often from development along the coast or as a result of clearing land for agriculture. As you know, corals are threatened by turbidity because their zooxanthellae need high light levels in order to photosynthesise. Sediment can cause large-scale destruction of reefs – for example, the islands of Okinawa to the south of Japan used to have reefs comparable to the Great Barrier Reef, but after the Second World War the islands were stripped of their vegetation for pineapple growing, and the increased sediment in run-off from the islands all but wiped out the reefs.

Question 7.7 Development also threatens coral reefs because sewage and agricultural activity result in increased nutrient supplies in coastal waters. Thinking back to Sections 4.2 and 4.3, and Figure 3.4 (the satellite image showing the colour of water around the British Isles), can you suggest why increased nutrient concentrations pose a threat to corals? ◀

In this chapter, we have been considering coral reefs as if they were independent habitats, but of course this is not the case. For example, in many tropical areas, reefs lie offshore from mangroves (seen in 'Tidal Seas', sequence 17). These form nursery areas for many reef fish and play a vital role in trapping sediment, preventing it from damaging the reefs. When mangroves are destroyed for development or (often) shrimp farming, coral reefs may be smothered with sediment and killed.

Reefs and their inhabitants are also under serious threat from direct onslaughts on the habitat. As the reefs are made up largely of calcium carbonate (i.e. limestone), they may be exploited for building materials, obtained by dynamiting the reef. Dynamiting is also used as a crude fishing technique, along with indiscriminate use of cyanide. This disturbing topic will be looked at again in 'Deep Trouble', in the final part of the course.

While legislation and change of attitude could in theory prevent or limit damage to reef ecosystems by people, there is little we can do to control the climate. We know from recent climatic fluctuations that corals are very vulnerable to changes in environmental conditions. During the climatic fluctuations known as El Niño events, warm, nutrient-rich water invades the eastern tropical Pacific, and areas that are usually dry receive extremely heavy rainfall. Corals around the Galápagos islands (cf. Figure 5.8) have fared very badly, partly because of the lowered salinity of surface waters brought about by the heavy rainfall, and partly, it seems, because of the increased water temperature.

When water temperatures exceed 28 °C, zooxanthellae lose their photosynthetic pigment and become less productive. Corals atrophy, the zooxanthallae die or are expelled from the corals in streams of mucus, and the corals – now devoid of pigment, or 'bleached' – may themselves die. During the 1982–83 El Niño event, many Galápagos corals suffered bleaching, and by the end of 1983, 95% of these had been destroyed. Their demise was hastened by the activities of other organisms. Bleaching corals were quickly colonised by filamentous algae, which spread over

corals and rocks down to a depth of 20 m. Sea-urchins fed on this algae, at the same time eroding the coral. As the El Niño event waned, new coral larvae began to settle and become established, but for a colony to survive, the addition of new coral organisms has to keep pace with erosion by foraging sea-urchins and other coral grazers such as parrotfish, surgeonfish and damselfish. The activities of these grazers meant that some reefs have never recovered.

Many climate scientists expect that the recent trend of more frequent El Niño events will continue along with increased global warming, in response to rising concentrations of carbon dioxide in the atmosphere. This does not bode well for coral reefs. What is more, there is strong evidence to suggest that the increase in carbon dioxide in the atmosphere will of itself eventually lead to a global decline in coral reefs. An increase in the concentration of carbon dioxide in the atmosphere is leading to an increase in the amount of carbon dioxide in the oceans, and this in turn is gradually increasing the acidity of seawater. The more acid the seawater, the harder it is for corals to extract the carbonate ions they need to precipitate their calcium carbonate skeletons.

Although reef-building corals are likely to be the worst affected, there will probably also be negative effects on other marine organisms that make hard parts of calcium carbonate (e.g. shells and plates). These could include planktonic organisms (e.g. coccolithophores, Figure 1.9), as well as molluscs and echinoderms. Cold-water corals are also likely to be adversely affected, even before they have been fully explored. These side-effects of acidification need to be borne in mind when evaluating the idea of using the deep ocean as a site for 'sequestering' carbon dioxide produced by power stations.

However, the fact that reef-building corals could no longer build skeletons would not necessarily mean their extinction. It is possible that they could continue as non-reef-builders, and eventually, perhaps many thousands of years hence, reef-building could begin again.

8 Polar seas

'Frozen Seas' concentrates very much on marine mammals, which we will discuss in some detail later. However, first we should look at what we mean by 'polar' or 'frozen' seas.

8.1 Arctic and Antarctic: poles apart

The Arctic and Antarctic regions are geographically completely different (Figure 8.1): the Arctic is a largely enclosed ocean, with a very narrow connection to the Pacific (through the Bering Straits) and a somewhat larger connection to the Atlantic via the Nordic Seas and the Fram Strait. By contrast, at high southern latitudes the Southern Ocean encircles the continental landmass of Antarctica (which in places extends as far north as ~ 65° S).

The continent of Antarctica is the coldest place on Earth (cf. Figure 2.1). Its extremely low temperatures are partly the result of its position over the South Pole, but are also a result of much of its icy surface being thousands of metres above sea-level. There is yet another reason, related to the ocean.

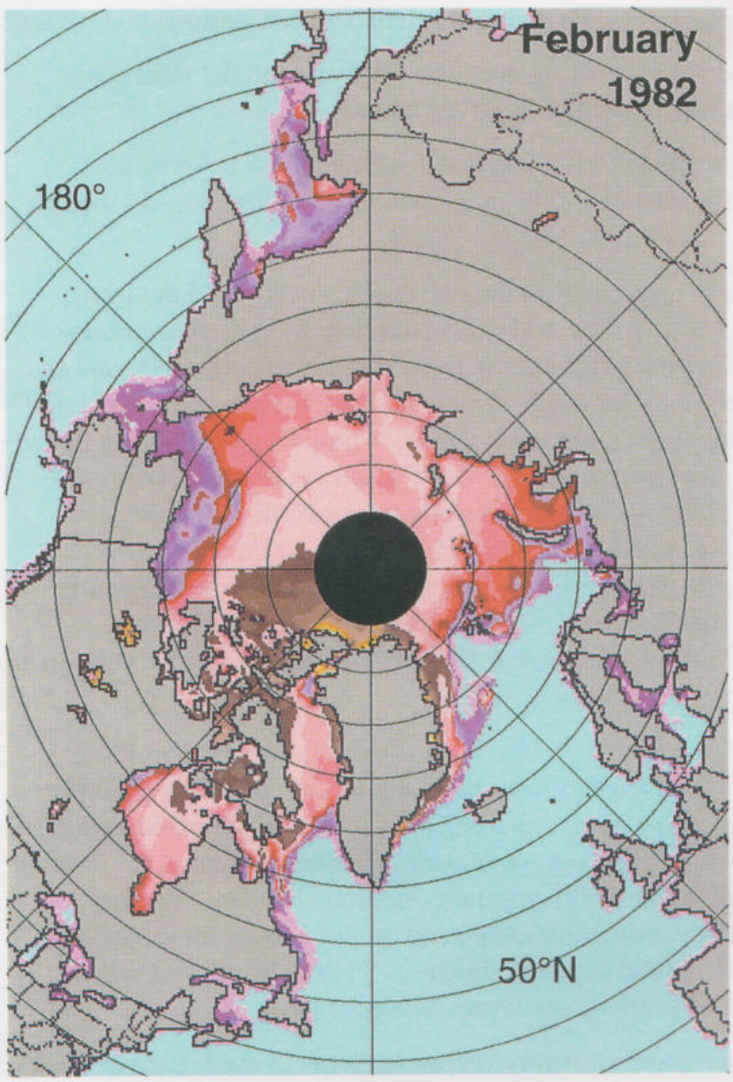
- By looking back at Figure 5.2, can you suggest why the pattern of ocean currents *also* contributes to Antarctica being colder than the Arctic?
- In the Northern Hemisphere, poleward-flowing currents – in particular, the Gulf Stream, and its extension, the North Atlantic Current – carry heat to polar latitudes. In the Southern Hemisphere, by contrast, the great size of Antarctica, and the broad (cold) Antarctic Circumpolar Current that flows around it, prevent warm currents (e.g. the Agulhas Current and the Brazil Current) from penetrating much further south than 50–55° S.

In fact, there is some transport of warm water southwards, and of cold water northwards, by means of eddies or rings like those which transfer water across the Gulf Stream (Figure 5.9), but as far as heat transport in ocean currents is concerned, the Antarctic continent is largely isolated.

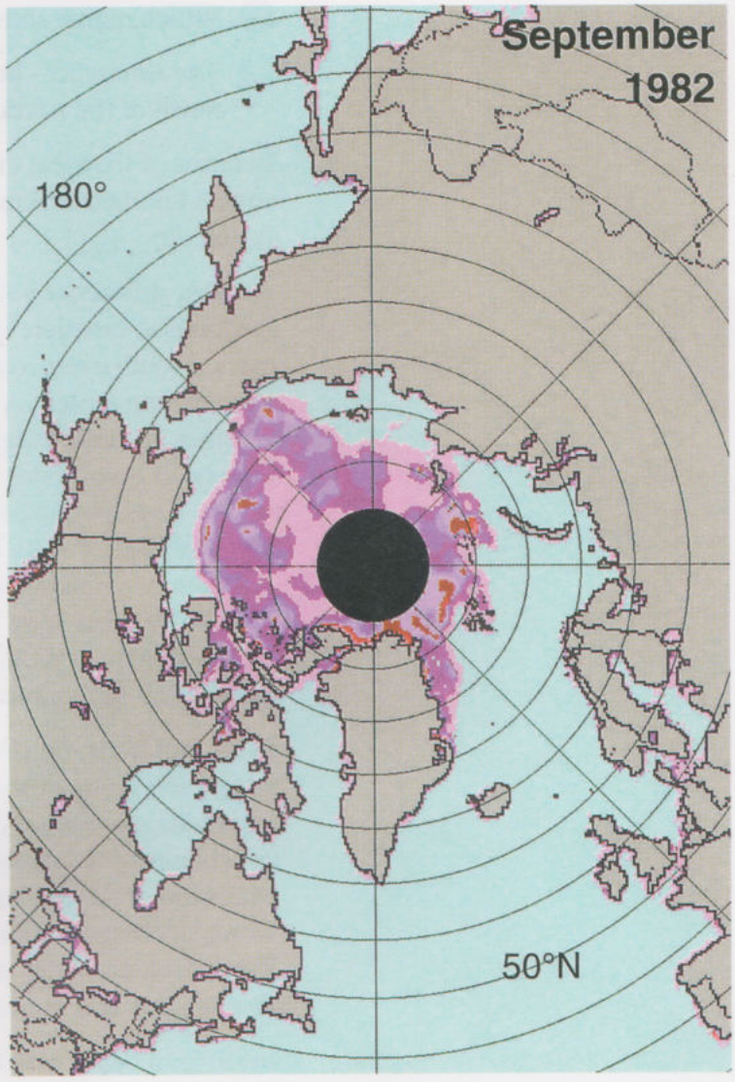
Sea-ice is formed by the freezing of seawater. Ice crystals are almost pure water, so their formation increases the concentration of salt in the seawater that is left behind. Young sea-ice therefore contains droplets of brine, but because salty water remains liquid at lower temperatures than pure water, these droplets gradually melt their way through the ice into the seawater below. As a result, old sea-ice is nearly pure water.

As a result of the contrasting settings of the Arctic and Antarctic, the ice cover of the two regions is very different, as is the amount that the ice-extent changes over the course of the year. Figure 8.1 shows the seasonal differences in the extent of sea-ice in the Arctic and Antarctic, as measured in 1982. The first thing to note is that the Arctic Ocean is largely covered by floating sea-ice or pack-ice.

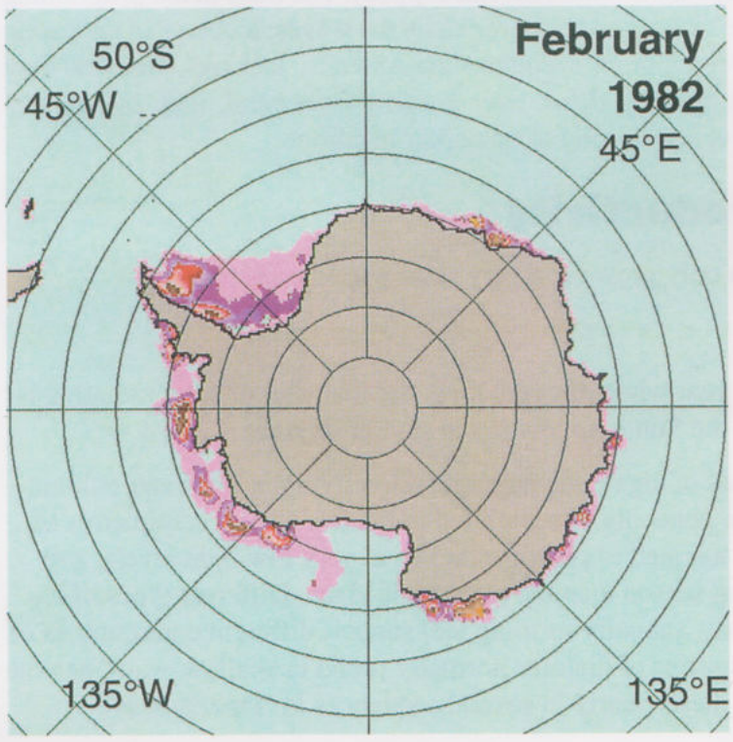
Figure 8.1 Seasonal changes in sea-ice cover in northern and southern high latitudes, determined using data collected by the *Nimbus* satellite programme in February and September, 1982. (a) and (b) show near-maximum and near-minimum ice cover in the Arctic, and (c) and (d) show near-minimum and near-maximum ice cover around the Antarctic. Purple and red correspond to complete or near-complete ice cover, pale blue corresponds to low or zero ice cover. (The orbit of the satellite is such that no data can be collected immediately over the pole, hence the black area in the centre of images (a) and (b).) Lines of latitude (shown as circles when looking down on the poles) are every 5°. *Note* In both polar regions, the maximum and minimum extents of sea-ice cover may vary markedly between one year and the next. These satellite images are fairly typical of the situation until relatively recently, but there seems to be a trend towards reduced sea-ice cover in the Arctic, and in parts of the Antarctic (see Section 8.6).


February
1982
180°
50°N

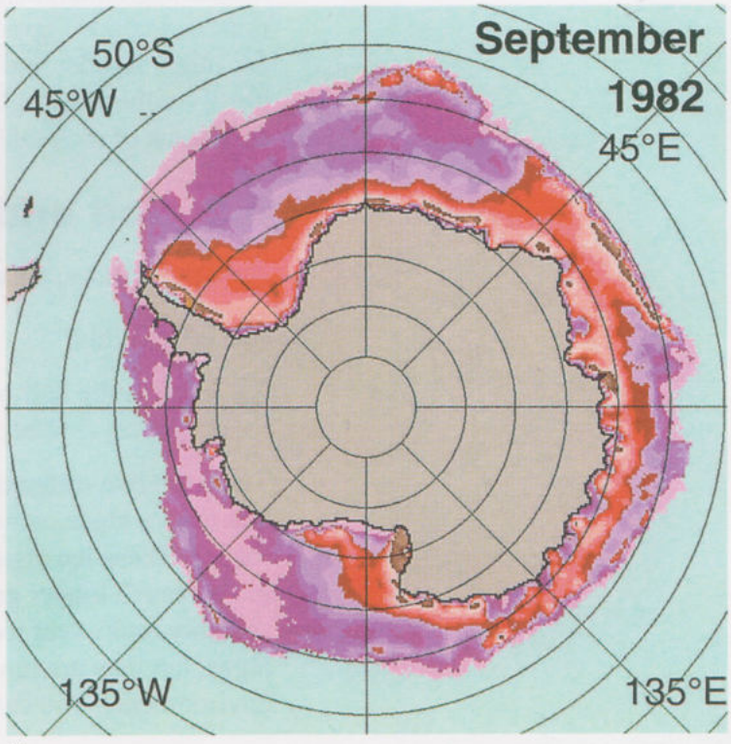
(a)


September
1982
180°
50°N

(b)


50°S
45°W
February
1982
45°E
135°W
135°E

(c)


50°S
45°W
September
1982
45°E
135°W
135°E

(d)

Which region shows the greatest change in ice extent between summer and winter?

The Antarctic – here the ice edge shifts over about 15° of latitude, whereas in much of the Arctic it moves over only 5–10° of latitude.

In terms of ice area, this corresponds to an increase from about 8.5 to 15 million square kilometres (km^2) in the Arctic, and from about 4 to 20 million km^2 in the Antarctic.

Another difference between sea-ice cover in the two regions is how old the ice is. Ice tends to circulate in the Arctic for several years, and only a small proportion is carried south every year. It moves in response to the ocean currents beneath, and (on shorter time-scales) in response to the wind; as a result, the ice-floes jostle and grind together, or 'raft' over one another. Sometimes, the ice is pulled apart, forming linear regions of open water, or leads (pronounced 'leeds'). When the leads refreeze, and the ice-floes are pushed together again, 'pressure ridges' can form. These may be 10–30 m high, but are actually several times thicker than this, as they also have 'keels' extending down into the water (you will be able to see some pressure-ridge keels in 'Frozen Seas'). For these reasons, and the additional ice provided by snowfall, Arctic 'multi-year ice' (as it is called) can be quite thick, even in those areas that are ice-covered for only part of the year.

In the Antarctic, by contrast, the sea-ice is largely re-formed from seawater every winter and melts every spring. Given this information, you may well be wondering where the enormous Antarctic icebergs come from. The answer is that these icebergs are chunks of the Antarctic ice-shelf that have broken off. The ice-shelf is the floating extension of the glaciers which flow down from the Antarctic ice-cap – in other words, icebergs are *land ice* (i.e. originally snow) and do not form from seawater. If you look carefully at the Antarctic icebergs shown in 'Frozen Seas', you will be able to see some indications of yearly snow layers within them.

In 'Frozen Seas', you will see some strangely shaped icebergs in the Southern Ocean. In fact, because they have broken off from the ice-shelf, large newly 'calved' (i.e. newly broken off) Antarctic icebergs are tabular (i.e. flat-topped). The ones in the programme must have tipped up at some stage, and been eroded by the waves. Icebergs in the Arctic are much smaller and tend to be more irregular than Antarctic icebergs. Because they mostly calve from glaciers moving down over Eastern Greenland, they often carry fragments of rock and gravel and so tend to be darker in colour.

8.2 Ice and productivity

At high latitudes, algae can only grow for a very short period each year.

Why is this?

Even in the half of the year when days are long, the intensity of solar radiation is relatively low because the Sun is so low in the sky (cf. Figures 4.2 to 4.4).

There are two different kinds of algae: the phytoplankton living in the water column and the ice algae, which are generally concentrated in the lowest few centimetres of the ice. These ice algae are adapted to photosynthesise at very low light levels, and have a much longer growing season than the planktonic algae. Different types of ice (notably multi-year ice versus annually forming ice) support different communities of algae, but they are mostly species of diatoms normally found in shallow-water benthic environments. You can see these clearly in several sequences in 'Frozen Seas'.

The ice algae use nutrients which leach down through the ice in the droplets of concentrated seawater, and from dust and other particles deposited from the atmosphere onto the surface of the ice. The ice algae are grazed by small invertebrates, as well as swarms of large copepods and amphipods, which in turn are eaten by Arctic cod and other fish (see later). In the Antarctic, ice algae are the main food source for krill overwintering under the ice. (You may remember the krill 'staining the sea red' in the introductory programme – you will see krill feeding on ice algae in 'Frozen Seas'.)

Ice clearly cuts down the primary productivity of the water beneath, especially when there is also a covering of snow. Under the thick Arctic pack-ice, it is always too dark for planktonic photosynthesis to occur.

However, in spring and summer, along the margins of the ice, the opposite is true. For centuries, navigators have recorded how, as their ships drew near to the ice-edge, they observed a marked increase in the numbers of whales, seals and birds. In the Southern Ocean, the zone of high productivity can be clearly seen to follow the retreating pack-ice; this also occurs in Arctic waters but the effect is not as marked.

The melting ice produces a layer of low-salinity water, perhaps 50–75 m thick. Where the low salinity water meets the adjacent water, there is a front, and some of the causes of the high productivity may be similar to those that occur at other fronts (Section 5.4). The main reason, however, is probably that the less dense, low-salinity water floating on markedly more dense water beneath is a very stable situation.

By reference to Figures 4.9 and 4.11, can you recall why such a stable situation would favour a phytoplankton bloom when surface waters were no longer shaded by ice?

A stable upper water column favours a bloom because it means that phytoplankton are in less danger of being carried down out of the photic zone. In effect, the bottom of the low-salinity (i.e. low-density) layer acts as a 'floor' to downward mixing.

High productivities are also found in upwellings around glaciers entering deep water and around large icebergs.

Thinking back to Section 5.4.2, can you suggest any possible mechanism for upwelling in the vicinity of glaciers entering deep water?

One possibility is that subsurface currents, carrying water with high nutrient concentrations, are forced upwards by the presence of the glacier tongue, rather in the way that water is deflected upwards at shelf break fronts.

Icebergs have most of their volume underwater and could in theory act like small islands (Section 5.3), were it not for the fact that they are carried along in the water. In fact, so much of their bulk is under water that they tend to move with *subsurface* currents. As discussed in Section 5.2, wind-driven flow at depth is at a greater angle to the wind than surface wind-driven flow, so icebergs move at an angle to the direction of surface flow. When an iceberg is surrounded by pack-ice, it may be clearly seen to be moving *across* the direction in which the ice is moving. Therefore, it is the upper layers of water that are disturbed by the passage of the iceberg, which stirs nutrient-rich water up into the photic zone.

Upwelling of deeper water is thought to be responsible for the high productivity of extensive areas of open water within the pack-ice, known as *polynyas* (pronounced

'poleenyas'). Polynyas tend to occur in more or less the same place each year, and in the Arctic they are often connected by linear open channels known as shore leads. They seem to be maintained at least partly by current patterns, and the upwelling that makes them such biologically productive regions may also play a part in keeping them open. In polar regions, water at depth is generally warmer than that at the surface, and a supply of upwelled warm water could keep the polynyas open. (It is possible for cold seawater to lie above warm seawater because the density of seawater is determined by its temperature *and* its salinity. The relatively low salinity of surface water, mentioned earlier, allows it to be sufficiently less dense to float upon warmer, more saline water.)

As you will see in sequence 2 of 'Frozen Seas', polynyas provide winter refuges for whales, and feeding places for walruses and polar bears; some species of seal also congregate in polynyas.

8.3 Coping with cold

Around Antarctica and in the waters at northern high latitudes, temperatures are always low, and in winter often hover just above the freezing temperature of seawater at –1.9 °C. However, we should not fall into the trap of thinking that the polar regions are necessarily a more harsh environment than any other. The animals that live there have evolved to suit their surroundings and the food available to them, just as animals living in less extreme environments have done.

However, the possibility of freezing does present a problem for animals in polar seas in winter. Even if the animal were not killed by the cold itself, the formation of ice crystals could damage the soft tissues, both through mechanical damage, and because the formation of crystals of pure water from salty body fluids would raise the salt content of the body fluids that remained.

The presence of dissolved salts in water lowers its freezing temperature (this is why salt is often put on icy roads). Nevertheless, in winter, surface polar waters may cool to their freezing temperature and to the freezing temperature of the body fluids of many invertebrates and fish.

By reference to Section 2.1.2, can you explain why teleost fish (i.e. bony fish) are at a greater risk of freezing than are sharks and rays, and most marine invertebrates?

Elasmobranchs, and most marine invertebrates, have blood and body fluids with salt concentrations comparable to those of seawater. Teleosts, by contrast, have blood with salt concentrations only 30–50% of that of seawater. The blood of teleosts therefore freezes at higher temperatures than the blood of elasmobranchs and of most marine invertebrates.

The bodies of deep-water fish out of contact with ice can be cooled below their usual freezing temperatures (i.e. they can be 'supercooled'), but fish living near the surface are at risk of freezing through drinking seawater containing tiny ice crystals, which can trigger freezing in their body fluids. The ice-fish, seen in 'Frozen Seas', is shallow-living but survives because it produces a kind of antifreeze which lowers the freezing temperature of its body fluids.

As you know, most marine mammals maintain their body temperatures at about 38 °C, by means of their high metabolic rate and by adaptations that favour heat conservation (Section 2.1.2). The areas of the body most prone to heat loss are the

limbs or flippers, where a relatively large surface area is exposed to the cold water. Dolphins have an adaptation to reduce heat loss from their flippers which has similarities with the heat-conservation adaptation found in tuna (Section 6.4.1). Arteries carrying warm blood to the flippers are surrounded by veins within which blood is carried back into the core of the animal. Heat passes from warmer artery to cooler vein, and so is conserved within the dolphin.

8.3.1 Life on the sea-bed in polar regions

The Blue Planet programmes do not include any sequences of benthic life in the Arctic or Antarctic, so we will only say a little about it here. Although the spring bloom is short, the organic debris that rains down onto the sea-bed below is sufficient to support as rich a benthic fauna as in other parts of the globe. In very deep water, off the continental shelf, animals are similar to those in other parts of the deep ocean, as conditions are very similar (we will look at the deep-sea benthic environment again in Chapter 10). On the continental shelf (e.g. in the Weddell Sea off Antarctica) many of the invertebrates are similar to their temperate counterparts, but because of the cold they have very slow metabolic rates and grow slowly, often attaining great size.

However, the shallow subtidal sea-bed is very different from that at lower latitudes (as shown in Figure 3.5, for example). At the highest latitudes in winter, benthic organisms may be killed by ice forming on the sea-floor, as a result of water being supercooled at the surface, sinking and forming ice crystals around the animals. Also, land-fast ice – i.e. ice attached to the land, also known as fast ice – may have a deep 'foot', and continual motion of this can completely clear the sea-bed. There is little chance for life to establish in summer either, as ice-floes and icebergs gouge and scrape the sea-bed, so that it is simply bare sediment.

8.4 Marine mammals

Marine mammals play a particularly prominent role in 'Frozen Seas', so this seems an appropriate place to say a little more about them. There are three groups of marine mammals:

1 Whales and dolphins, which belong to the Order Cetacea (Figure 1.8).
2 Seals, elephant seals, sealions and walruses which belong to the Order Pinnipedia, and their distant relations, the sea-otters.
3 Manatees, dugongs and sea cows, which belong to the Order Sirenia.

Sea-otters (shown in sequence 4 of 'Seasonal Seas') belong to the Mustelidae, the family which includes otters and badgers. The Sirenia live in warm waters and are herbivorous. Sightings of these animals may have been the origin of the old sailors' belief in mermaids (or sirens). We will not say any more about them here.

8.4.1 The wing-footed ones

Seals, elephant seals, sealions and walruses are known as pinnipeds, which means 'wing-footed' (*pinna* = feather or wing).

There are two families of seals, the so-called 'true seals', which have visible earholes, and 'eared seals', which have small ear flaps. True seals have a short neck and their overall body shape is sausage-like. They swim by powerful side-to-side movements of their hindquarters (like otters), using their short backward-pointing webbed hind

limbs for propulsion in water, rather like a fish's tail. The hind limbs are of no assistance for moving about on land, where true seals are very ungainly. Both hind and front flippers are fur-covered, and the front flippers (which are short and thick, with blunt claw-like nails) are used for steering underwater.

Eared seals have longer necks than true seals, and powerful sloping shoulders. They swim by making long sweeps of their long, leathery foreflippers, either 'flying' through the water like a penguin, or 'rowing' themselves along. Their hind flippers do not seem to be used in sustained swimming, except perhaps as a rudder for steering, but they are webbed and when spread out can be used like paddles, for manoeuvring. The most obvious difference from the hind limbs of true seals is that they can be rotated forward for moving about on land, or for sitting on.

Walruses have a swimming style intermediate between those of eared seals and true seals, but generally have more similarities with eared seals. In terms of evolution, eared seals and walruses are an older group than true seals, having diverged from the stock of dog-like mammalian carnivores about 10 million years earlier – about 25 million years ago, compared with 15 million years ago for true seals.

Question 8.1 Given that sealions were formerly used as performing animals in circuses, would you say they are true seals or eared seals? (Swimming sealions can be seen in sequence 4 of the introductory programme.) ◀

The remainder of the eared seals are species which we generally refer to as fur seals because of their abundant underfur. They are generally smaller than sealions, and have longer flippers and blunter noses.

In size, appearance and behaviour, eared seals are a much more uniform group than true seals. With notable exceptions, they mainly live in cool-water regions, and none of the species breed on ice. They tend to live in highly productive areas, and are mostly generalist feeders, eating a variety of nektonic and benthic organisms, both fish and invertebrates, whichever is most easily available. In all species of eared seals, the male is substantially larger than the female – although elephant seals (which are true seals) also have a great disparity in size between the sexes.

True seals probably originated in warm waters, but are now found mainly in high latitudes. Many breed on ice, and have white pups. They are specialist feeders, so avoiding competition between the different species. For example, in northern polar seas, the ringed seal (which breeds on fast ice or heavy pack-ice) feeds on small fish and planktonic crustaceans, while spotted and ribbon seals (which use slightly thinner pack-ice) feed on shallow-water fish, and on deep-water fish and squid, respectively. Unique amongst the true seals, the bearded seal feeds on benthic molluscs and crustaceans. In southern polar seas, the Weddell seal (which you will see in 'Frozen Seas') feeds on fish below the Antarctic ice-shelf, sometimes diving down to 600 m in pursuit. Another deep-diving seal is the Ross seal, which lives in the pack-ice and feeds on deep-water squid. The 'crabeater' seal (perhaps the most abundant Antarctic species) eats krill, which it strains through its many-pointed teeth (as does the Antarctic fur seal, an eared seal). Elephant seals feed only on squid, and the magnificent leopard seal is a top predator, taking other seals and penguins.

Pinnipeds generally have large eyes, sometimes very large indeed. They do not have a duct to carry tears away from the eye, so may have tears running down their faces, adding to their apparently doleful expressions. They can see clearly in both air and water and their eyes are adapted to avoid excessive accommodation (adjustment) in

moving from one to the other. Their retinas are adapted for low light intensities, which means that there is no colour vision. Like a cat's, the retinas are backed by a shiny surface which reflects the light back through the sensory cells a second time.

8.4.2 Whales

Of all the aquatic mammals, the whale is the one which has most completely severed its links with the land and has become a supreme performer in the sea. Even the pinnipeds need to haul out onto land or ice to breed, and cannot compete with whales when it comes to swimming and diving. Whales and dolphins are known as cetaceans, which comes from *ketos*, the Greek for whale. Dolphins, like killer whales, are toothed whales.

How did the whales we know today evolve?

65–50 million years ago, all of the mammals in existence lived on land, so it is clear that aquatic mammals must have evolved from terrestrial mammals. Until recently, all the known fossil remains of early cetaceans indicated an amphibious or wholly aquatic lifestyle, but fossils found in Pakistan (of an animal which has been named *Pakicetus*) now provide a link between recent and present-day whales and the oldest known group of 'even-toed ungulates' – a group of hoofed mammals which today includes hippos, cows, pigs, camels and giraffes. The significant link between *Pakicetus* and early ungulates (e.g. an animal known as *Diacodexis*, Figure 8.2 overleaf) is in the ankle bones, which are of a type suitable for efficient running. Although these ankle bones link *Pakicetus* with animals like modern-day hippos, they indicate that modern whales are *closer* to the early ungulates than they are to modern hippos, cows etc.

Figure 8.2 shows the likely evolutionary route from animals like *Diacodexis* to modern whales. *Ambulocetus* ('walking whale') was amphibious. It may well have moved around like a large sealion, and may perhaps have swum rather like an otter. *Dorudon* was fully aquatic and more streamlined, with greatly reduced pelvis and hind limbs.

There has been much debate about the relationship between the baleen whales (Mysticeti) and the toothed whales (Odontoceti) (cf. Figure 1.8). It used to be thought that these two groups became separate about 40 million years ago, and it was assumed that the specialised carnivore teeth and associated jaw structure of the toothed whales and the dolphins marked them out as evolutionarily distinct from the baleen whales, which live mainly on zooplankton. However, recent work involving DNA sequencing suggests that baleen whales are closely related to sperm whales, which have teeth, whereas the dolphins seem to be a separate group. This suggests that the baleen whales' highly specialised plankton-feeding lifestyle arose relatively recently – perhaps only 25 million years ago.

Modern whales

The bones of modern whales are light and spongy. They do not have to support the weight of the animal, and need only to act as anchor points for the muscles. In the case of the baleen whales, the skulls have been extremely modified in shape, and instead of teeth there are two rows of plates (known as baleen plates) which hang down from the roof of the mouth. As mentioned in connection with the blue whale in the introductory programme, the inner edges of these plates are fringed with bristles ('whalebone'), and the whale feeds by using the bristles to sieve zooplankton from huge mouthfuls of water; it then collects the food from the fringes with its tongue.

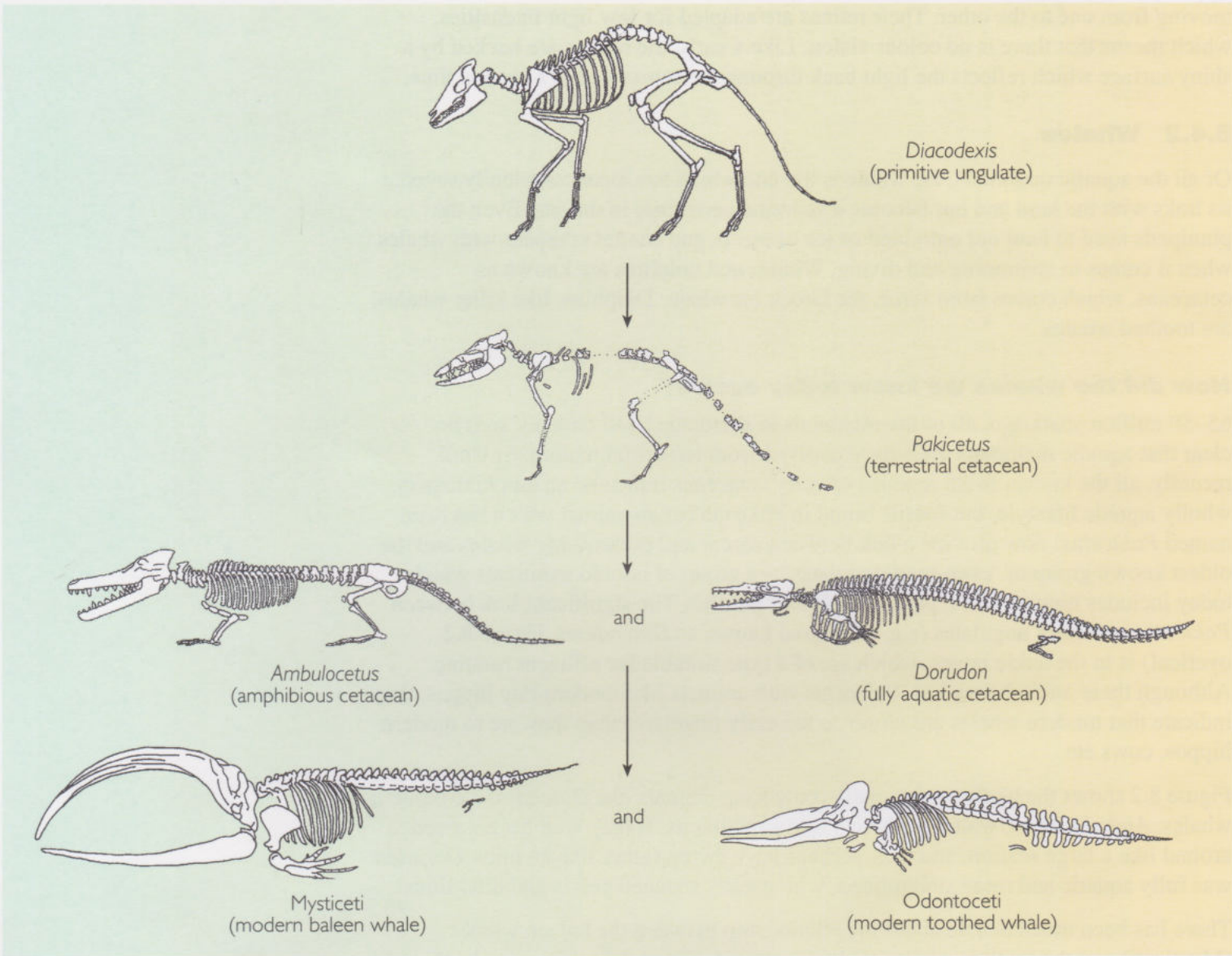


Figure 8.2 The most likely evolutionary route from terrestrial ancestor to modern whales. *Note*: *Ambulocetus* and *Dorudon* are just two representatives of the cetaceans which evolved from *Pakicetus*. (Skeletons not drawn to scale.)

As the relationships between different types of whales can be rather confusing, Table 8.1 summarises the different families of baleen whales and toothed whales. As mentioned in the notes for the introductory programme, the rorquals are those baleen whales that have expandable grooves in their throats, which allow them to engulf huge volumes of water containing large numbers of zooplankton (or occasionally, fish).

Question 8.2

(a) What is the largest member of the Mysticeti?

(b) In what sense is a killer whale a dolphin?

(You may find it useful to consult Table 8.1 and/or look back to Figure 1.8.) ◀

Figure 8.3 has been included to show the relative sizes of different groups of whale, as it is not easy to judge the size of animals on film. This diagram was compiled some years ago, and many of the larger whales were drawn on the basis of photographs of corpses of whales killed during whaling.

Table 8.1 Families of baleen and toothed whales (including species seen in the Blue Planet programmes); see also Figure 1.8.

Baleen whales

Gray whale: 1 species

Rorquals: 6 species – blue whale, finback whale, Sei whale, Bryde's whale, minke whale and humpback whale

Right whales: 3 species – right whale, pygmy right whale and bowhead whale

Toothed whales

Dolphins: 32 species, including common dolphins, bottle-nosed dolphins, spinner dolphins, pilot whales, killer whales

Porpoises: 6 species, including harbour (or common) porpoise

White whales: 2 species – beluga and narwhal

Beaked whales: 18 species, including bottle-nosed whale

Sperm whales: 3 species – sperm whale, pygmy sperm whale and dwarf sperm whale

River dolphins: 5 species

You have now seen quite a few DVD sequences showing whales, either feeding or swimming. Why are the drawings of the rorqual baleen whales in Figure 8.3 somewhat misleading?

A swimming rorqual is as streamlined as a toothed whale, because the throat grooves are contracted (cf. the blue whale in the introductory programme). When a rorqual is feeding, however, the grooves expand and the throat bulges outwards in a more exaggerated way than shown in Figure 8.3 (cf. the rorqual at the very end of 'Bounty off Natal').

It should be said that even photographs and film of large whales do not produce entirely accurate images, because the wide-angle lenses needed to 'capture' the whole animal make them look slimmer than they are in reality.

As Figure 8.3 shows, the only toothed whale which comes near to the size of baleen whales is the sperm whale, with its enlarged head. As you may remember from 'Wild Moves: Water' (sequence 11), most of this large volume is occupied by the spermaceti organ, which plays a significant role in enabling the sperm whale to be the champion diver amongst marine mammals. Sperm whales are known to dive to 1000 m or so to catch squid, but from the contents of their stomachs – including stones and tin cans, as well as bottom-living sharks – it is obvious they sometimes actually feed on the bottom. However, the most impressive thing about their diving is not how deep they dive, but how efficiently they do it.

It seems that as the whale dives down out of the warm surface layer, the spermaceti is cooled by an intake of water through the blowhole. This cools the wax so that it solidifies and shrinks, thereby increasing the density of the head and enabling the whale to sink fast. When the whale has finished feeding, it warms the spermaceti by increasing the flow of blood through the capillaries in the front of the head. The wax warms slightly, melts and becomes less dense, and the increased buoyancy allows the whale to rise to the surface with a minimum of effort.

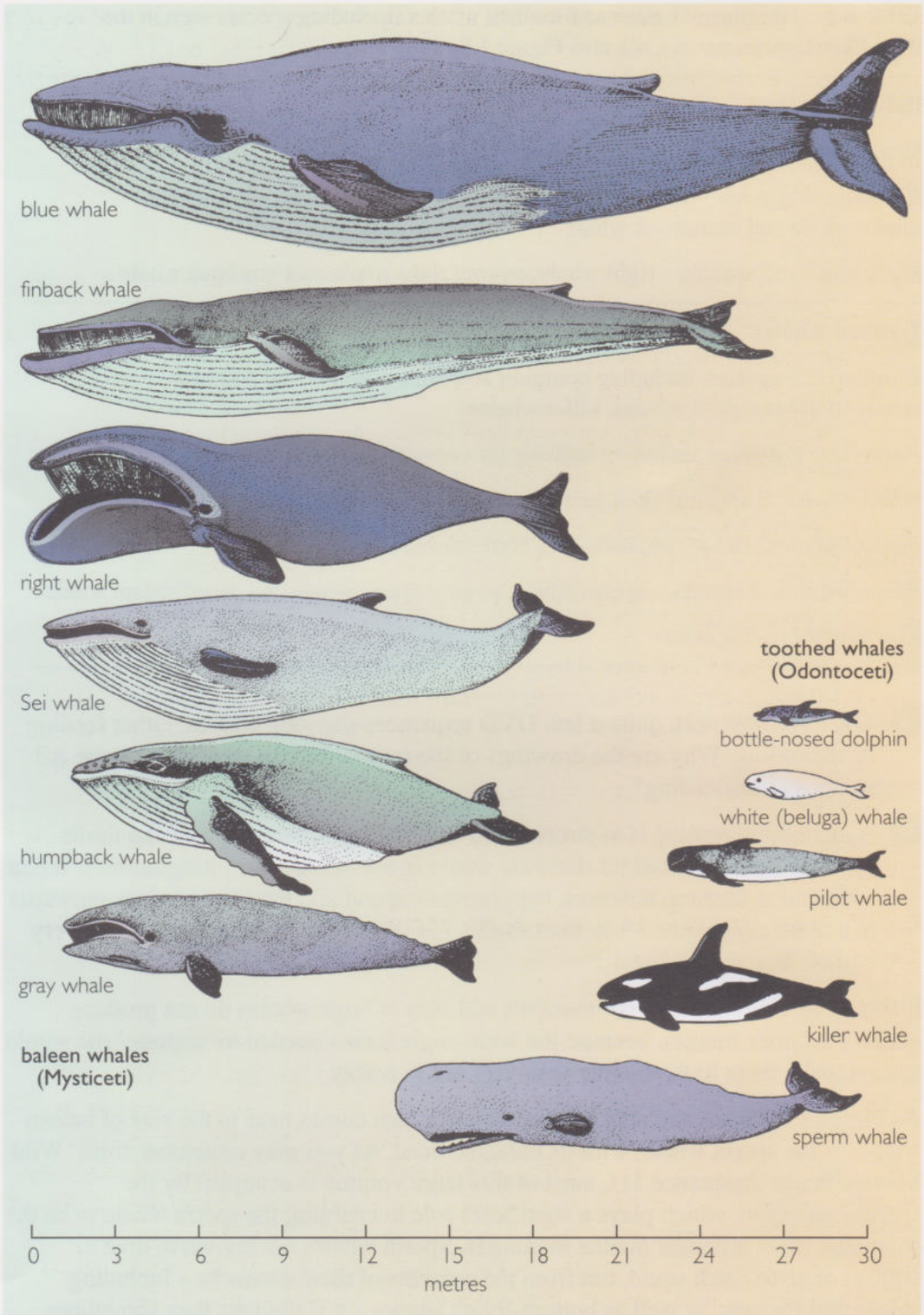


Figure 8.3 Relative sizes of baleen and toothed whales. (Note the caveat in the text.)

When a whale dives, its lungs compress and the air in them is driven into the windpipe and its branches, and the extensive nasal passages. As the whale rises to the surface, the lungs gradually expand, the blowhole is opened wide and the foul air that has accumulated during the dive is expelled as a cloud of spray. In fact, baleen whales have two nostrils each of which has a blowhole, so what appears to be one blowhole is in fact two parallel slits which are close together when shut. In toothed whales, the two nasal passages join together and there is only one nostril and one blowhole. Sperm whales are unique in that their blowhole is at the front of the head and to one

side, so that the spray is ejected forwards at an angle of 45°. This is a result of the fact that the two nasal passages have different functions, the right nasal passage being used to take in water to cool the spermaceti when diving (as described above), the left being used to clear out stale air.

In earlier chapters, it was suggested that while watching the DVDs you note down characteristics of how whales and dolphins swim, and of whale and dolphin behaviour generally.

- What is the most noticeable difference between how whales and dolphins swim and how fish swim?
- Whales and dolphins swim by moving their tails up and down; when fish swim, they move their tails from side to side.

Whales and dolphins use their flippers for steering, and the dorsal fin (if there is one) may be useful for stabilization (although it could also be used in temperature regulation). The flexibility of the whale's body is enhanced by the fact that the layer of blubber, which helps keep the body temperature at about 38 °C (Section 2.1.2) and may be 20 cm thick, is not tightly fixed to the underlying muscular tissues.

- How would you describe the way that toothed whales hunt for food?
- Toothed whales hunt cooperatively. There are several examples in the Blue Planet programmes: bottle-nosed dolphins catching mullet at the end of 'Tidal Seas', dolphins using 'bubble-netting' and driving sardines up to the surface at the beginning of 'Bounty off Natal' (sequence 2), and the killer whales (orca) battering herring with their tails, at the end of 'Seasonal Seas' (sequence 17).

Generally speaking, whales are very social animals, enjoying group interactions and even playing together.

8.4.3 The importance of sound for whales and other marine animals

How whales use sound

Another aspect of whale behaviour that you may have noted down is their extensive use of sound, both for communication and (in the case of toothed whales) for echo-location. Toothed whales are sensitive to sounds over a wide range of frequencies, and can distinguish different frequencies with great precision, being progressively better at this with increasing frequency (i.e. higher pitch). They produce a wide range of sounds, some like a continuous whistle (which seem to be for communication) and some as pulses. The pulsed sounds include trains of clicks (which may sound like a buzz) as well as sounds resembling barks, bleats, groans, moans, squawks, squeals and yelps. They also make short sounds when they leap or clap their jaws. Interpreting the significance of these various sounds is not easy because while the sounds made in different situations vary widely, the same sound may be produced in different contexts (e.g. escaping from danger, chasing food, sexual activity or play). This could indicate that the meaning of a sound is determined by its context, or that a particular sound is produced as a result of the same factor (e.g. excitement or stress) operating under different circumstances.

Trains of clicks are also used in echo-location, and toothed whales in general have highly developed echo-location systems. The waxy lens-shaped organ which focuses the sound – known as the 'melon' – is situated in the forehead, and focuses 'clicks'

produced in the nasal passages. The returning echoes are channelled to the inner ear along oil-filled sinuses in the lower jaw. The inner ear is insulated from extraneous sounds transmitted along other bones in the skull because it is within a bone that is suspended from the skull by a ligament, and is surrounded with a kind of foam. Toothed whales can identify the direction of the source of an echo or some other sound extremely accurately, to within an angle of a few degrees in both the horizontal and vertical planes.

The use of sound by the Mysticeti has not been as easy to study as that by the toothed whales, although whalers have long known of their acute hearing. The sounds are harder to classify than those of toothed whales, being much more variable. They tend to last longer, and are mostly of much lower frequency. Low-frequency sounds travel through seawater with less loss of energy than high-frequency sounds, and the main use of the sounds produced seems to be communication between individuals which may be very widely scattered. As mentioned in Section 4.6, whales may use the sound channel to communicate over 1000 km or more.

Perhaps the most famous whale sounds are the 'songs' of the humpback whale. Different populations have distinctive songs, although they gradually evolve with new motifs being added and others being dropped. Sometimes, the song of another nearby population may be adopted, apparently in preference. Within populations, individuals have their own voice characteristics which make their song distinguishable from that of other whales. Humpbacks migrate to warm waters to breed, and on arrival at the breeding grounds, the males begin to sing – the song of a male humpback could be heard in 'Coral Seas' (sequence 11).

Sound production and detection in other marine animals

Seals also have very highly developed hearing, and can hear well in air (as can dolphins in the case of certain types of sound). Communication by sound also seems to be widespread in fish, particularly for distinguishing their own species from other species. Fish often produce sounds in response to stimuli (e.g. when they are alarmed) or during reproductive activity. Like whales, fish can hear over a wide range of frequencies, but their ears are most sensitive to lower frequencies (longer wavelengths) which, as mentioned above, travel furthest in seawater. Fish with swimbladders, which resonate readily, may use muscles attached to the swimbladder to generate sound. As sound waves are pressure waves, and pressure affects the swimbladder, the presence of a swimbladder, and its position in relation to the inner ear (where sound is received), also affects the sensitivity of a fish to sound – you may recall that many deep-sea fish use their swimbladders to detect sound (Section 6.3).

What other way do fish have of detecting disturbances in the water, generated perhaps by the swimming actions of prey, or of an approaching predator?

Along their flanks, and on their heads, they have their lateral line system, with its many neuromasts, each carrying numerous sensitive hair cells (Section 6.5).

Finally, we should note that many invertebrates also produce sounds and are able to detect them – some particularly noisy crustaceans have been named 'snapping shrimps'.

Noise pollution in the ocean

Over recent decades, it has become increasingly obvious that noise produced by human activities in the ocean is having deleterious effects on marine animals, particularly whales and dolphins. As with chemical pollution of the seas (which we

began to take seriously a decade or so ago), some of the impacts are obvious, while others are more insidious.

There are three main causes of large-scale sound pollution in the oceans. The most widely dispersed source of loud noise is commercial shipping. At any one time, about 90 000 large vessels are crossing the seas, producing a continual low-frequency rumbling. It has been estimated that noise levels from commercial shipping have been doubling every decade or so, which means that today the oceans are about 30 times noisier than they were 50 years ago. Whales and dolphins have evolved over millions of years to use sound to enable them to function effectively – both as individuals and community groups – in the great expanses of the ocean. Over the course of a typical whale's lifetime, the 'fog' of shipping noise will have caused its acoustic world to shrink dramatically, down to one-hundredth or less of what it once was, effectively isolating it from other whales of the same species in waters which, although distant, were previously within communication range.

Shipping noise increases near the coast, particularly in the vicinity of ports and coastal industry. Such areas are also likely to impinge on productive coastal waters where whales feed.

- What other aspect of whale behaviour is likely to be disrupted by noise pollution, particularly in the case of male humpbacks?
- The singing of (low-frequency) mating songs, which can be drowned out by the deep rumbling from shipping.

Large baleen whales (including gray whales) are being forced to abandon their breeding and calving grounds. They have also been observed to change their migration routes, apparently as a result of shipping noise.

The second cause of serious sound pollution is also concentrated in productive coastal waters, although it is moving into deeper and deeper water. This is the exploration for oil and gas reserves under the sea-bed, which involves seismic surveys using air guns that produce underwater explosive pulses every 10 seconds. It is known that these explosions affect the behaviour of toothed whales (dolphins, sperm whales, etc.).

- Can you suggest what activities are likely to be affected in the case of toothed whales?
- Communicating by sound, and hunting using echo-location, are both likely to be disrupted.

Studies of sperm whales diving for squid indicate that air-gun noise interferes with their echo-location technique, especially when they are homing in on prey. More generally, it seems that air-gun noise makes whales (and fish) lethargic, so that they are less efficient at catching prey.

The third cause of serious sound pollution is less widespread and is sporadic rather than continual, but it is a threat to marine mammals because of the intensity of the sound. This source is sonar being used in naval military exercises. Mid-frequency 'tactical sonar', employed in anti-submarine warfare, employs loud mid-frequency 'pings', and has been linked to mass strandings of beaked whales (e.g. bottle-nosed whales). Dead stranded whales have been found to have gas bubbles in their blood, brain and other organs, and damage to their tissues, including haemorrhaging of blood vessels – symptoms similar to those of the decompression sickness suffered by human divers who surface too quickly. The deeper a whale (or any other mammal) dives, and

the longer it stays submerged, the more of the air in its lungs dissolves into the blood. It is thought that the pings cause a 'layer of sound' spreading out in the sound channel, which alarms whales swimming at depth, causing them to stay down too long, or to come up too fast.

Considerably louder than the pings used in tactical sonar are the low-frequency booms used in 'active sonar', to detect the latest generation of 'quiet submarines'. These sounds are close in frequency to the songs of male humpbacks, so to compensate for their songs being masked by booms, the humpbacks sing for much longer. This must have a cost in energy for the humpbacks, but it is not known what other effects the booms may be having on whales generally, as individuals or as communities.

▶▶ If you have not already done so, you should now watch 'Frozen Seas' on DVD 3. We recommend that you read the 'Activity' paragraph, and then watch the programme all the way through. You can then read the notes relating to individual sequences and play the programme again or, if you wish, replay individual sequences. ◀◀

Notes on 'Frozen Seas'

Activity During the programme, you will see (in this order): walruses, harp seals, hooded seals, ringed seals, walruses (again), Weddell seals, fur seals and leopard seals. For each of the seals, try to work out whether they are 'true seals' or 'eared seals'.

Sequence 1

- Here and later on in this programme, note the green colour imparted to the ice by algae living in it.
- The statement about a temperature of –50 °C is, of course, referring to *air* temperature on land.
- As you should now appreciate, the Arctic does *not* freeze from shore to shore each year, as the narration suggests. Most of the ice in the Arctic ice-cap is several years old.

Sequence 3 The hummocky nature of multi-year ice can be clearly seen during much of this sequence. In particular, the lair in which the ringed seal pup is hiding seems to be in the downward-extending part of a pressure ridge, i.e. the keel. As it swims away, you can see the keel quite clearly.

Sequence 5 Note the leads, which may later be transformed into pressure ridges if the ice-floes are driven together.

Sequence 6 Walruses use their tusks to stir up the sediment when they are hunting for molluscs, and also for hauling their great bulk up onto the ice.

Sequence 8 As explained in the text, most of the Arctic Ocean is covered by ice which survives from year to year (Figure 8.1a,b), and newly forming ice like that shown here would only be seen in areas where all the sea-ice had melted during the summer. Those areas are mostly around the edge of the Arctic basin, though in recent years there has been open water much further north (more on this in Section 8.6).

Sequence 10 The Antarctic ice shelf (the floating seaward extension of glaciers) can be seen in the background of the initial shot of the Weddell seal's breathing hole.

Sequence 11 Note that inside the krill, you can see the algae they have eaten.

Sequence 12 Note the two different ways that chinstrap penguins and emperor penguins leave the water: the former make use of waves, and the latter make use of their own buoyancy.

Sequence 13

- These fantastically shaped icebergs were once tabular but have tipped over, and have been sculpted by the sea into the shapes you see here.
- The minke whale seems to have algal growth on its body, and the humpback carries barnacles and other encrusting organisms. (You will probably have spotted other examples of whales providing living space for smaller organisms, in previous programmes.)

Sequence 14 In this sequence, you can see in the background sea-ice that has moved under the influence of wind and cracked, and the separate floes have then rafted over one another.

Question 8.3 On the basis of the scenes showing Antarctic fur seals pursuing krill (sequence 13), explain whether you would classify fur seals as true seals or eared seals. ◀

8.5 Food webs in frozen seas

As 'Frozen Seas' shows so dramatically, in both the Arctic and the Antarctic, mammals dominate the upper part of the food web, and are the top predators; while algae – both ice algae and phytoplankton (Section 8.2) – form the base of the food web.

Have a look at Figure 8.4, which shows a simplified food web for Arctic waters.

Can you pick out some of the feeding interactions shown in 'Frozen Seas'?

At the top can be seen a scenario similar to that at the start of the programme, with polar bears as top predator (to the left), and carrion-feeding Arctic foxes and birds (to the right). At the bottom left walruses can be seen feeding on benthic invertebrates (which would include molluscs). Bowhead whales and rorquals (as well as right whales) can be seen feeding on various types of zooplankton.

Question 8.4 (a) On the basis of the feeding interactions shown in Figure 8.4, what would you say is the key organism in the Arctic?

(b) What group of planktonic animals, which appear in a number of Blue Planet programmes (including 'Tidal Seas' and 'Seasonal Seas'), are completely absent from the food web in Figure 8.4? ◀

Arctic cod are an important food source for a wide variety of birds and mammals. Their importance in the Arctic food web results partly from the fact that they are adapted to live and feed in a wide range of habitats: at the surface and under the sea-ice; at the edge of fast ice; in shallow coastal waters in summer; and at depths of more than 900 m. They are distributed throughout the Arctic and are extremely abundant. During the long winter they are widely dispersed, but in summer they congregate into enormous schools – all the more convenient for the predatory seals, as well as for the summer-visiting belugas, narwhals and bowheads.

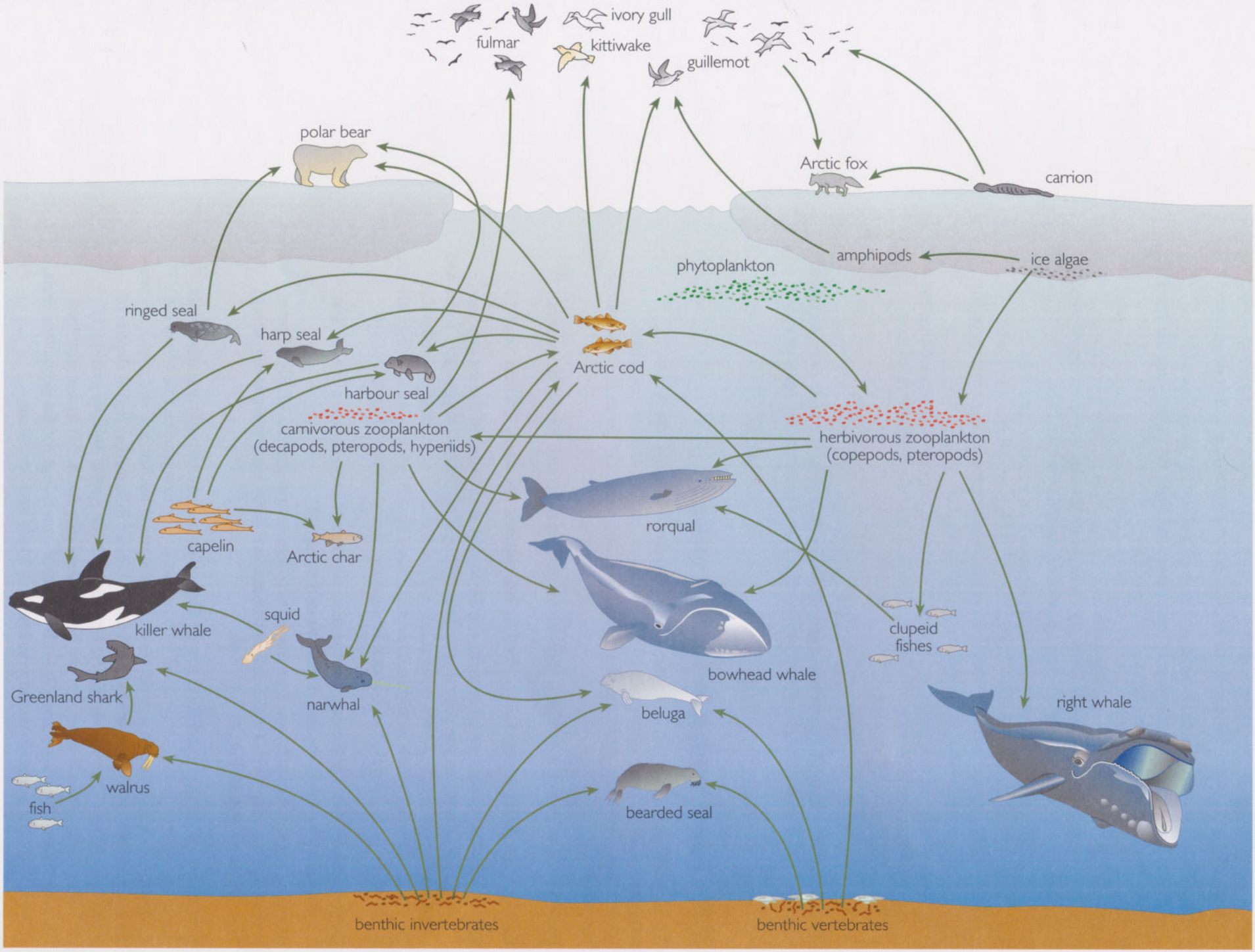

fulmar
ivory gull
kittiwake
guillemot
polar bear
Arctic fox
carrion
amphipods
ice algae
phytoplankton
ringed seal
harp seal
harbour seal
Arctic cod
carnivorous zooplankton
(decapods, pteropods, hyperiids)
herbivorous zooplankton
(copepods, pteropods)
capelin
Arctic char
rorqual
killer whale
squid
clupeid
fishes
bowhead whale
Greenland shark
narwhal
beluga
right whale
walrus
fish
bearded seal
benthic invertebrates
benthic vertebrates

Figure 8.4 *(opposite)* Food web for the polar seas to the north of the North Atlantic (the food web for high latitudes in the North Pacific differs from this in important ways). Note that this food web is simplified, and not all links and species are shown. (Not to scale.)

Sadly for the trapped beluga in 'Frozen Seas', the Arctic cod were still dispersed because it was too early in the year. The whales would not have been able to feed well, given that during the relatively brief dives they would have to go on wide-ranging forays, inefficiently collecting individual fish, and then come back to their ice-hole to breathe.

What would you say was the key component of the marine ecosystem at high southern latitudes?

It is, of course, the krill.

As mentioned in the notes for the introductory programme, the Antarctic krill is the species *Euphausia superba*. *Meganyctiphanes norvegica*, the species of krill (i.e. species of euphausiid) found in northern high latitudes, does not play such a pivotal role in the food web, and does not feed on ice algae.

As you know, in the Southern Ocean, Antarctic krill are the staple food of baleen whales and are consumed by certain species of seal (Section 8.4.1); they are also an important part of the diet for squid, fish and seabirds. In the final section of this chapter, we will look at why – unfortunately for these various predators – the dominance of *Euphausia superba* in the Antarctic ecosystem is under serious threat.

8.6 Frozen seas no longer?

As illustrated in 'Frozen Seas' (sequences 1, 8 and 9) and discussed earlier, the low temperatures of the polar regions are primarily a result of the low levels of solar radiation they receive. However, there is also another reason, namely that snow and ice reflect a large proportion of incoming solar radiation back to space – about 80–90% for fresh snow and ice. The high reflectivity of snow and ice, which reduces the amount of solar radiation that can be absorbed, is also known as a high *albedo*. If the snow and ice over an area of the Earth's surface melts completely, surfaces with a much lower albedo (e.g. rocks or the sea-surface) will be exposed, and these can absorb much more solar radiation. This increased absorption of heat leads to further melting, an even larger area with a lower albedo, and so on – a positive feedback effect. It was because of this positive feedback relating to albedo that polar regions were expected to be the first areas of the globe to show clear evidence of global warming – and so it has proved.

Of course, polar regions still receive low levels of radiation; they are warming because the atmosphere as a whole (and hence also the ocean) is warming. This is because increased concentrations of greenhouse gases in the atmosphere mean that more of the infrared radiation emitted by the Earth's surface (cf. the spectrum in Figure 4.7) is trapped by the atmosphere, so that less of it is lost to space than in pre-industrial times.

There is currently much concern about possible impacts of global warming on wildlife in polar regions. We will focus on different kinds of impacts in each of the two regions: in the case of the Arctic, certain negative effects are likely to result from human activity; in the Southern Ocean, the ecosystem itself already seems to be responding to warmer conditions.

The 'fragile Arctic'

The extent and thickness of Arctic ice has been closely monitored over recent decades, and the results do indeed show that Arctic sea-ice is thinning and penetrating less far south in winter. Warming is already causing problems for animals in the Arctic – for example, the sea in Hudson Bay has recently been freezing later and later each year, and the polar bears are having to wait longer before they can go out onto the ice to catch seals. However, it is important to note that on the basis of evidence from a relatively short period of time, it is not possible to be sure that this reduction in ice cover is part of a long-term trend rather than the result of a short-term climatic fluctuation.

The other serious threat to Arctic wildlife is more tangible. It seems highly likely that in the near future parts of the Arctic will be at increased risk of pollution associated with oil exploitation. Oil can be particularly damaging under cold conditions, because it does not disperse as quickly as it does at higher temperatures, and may also get trapped beneath and amongst ice-floes. The continental shelves around the Arctic Ocean contain huge reserves of oil and gas, the remains of phytoplankton that were buried by sediments and 'matured' over millions of years in anoxic conditions. At present, oil exploitation is technically impossible over much of the Arctic region. The permanent or seasonal ice cover prevents or hinders exploration and makes drilling extremely difficult and hazardous. In addition, until recently there were no suitable routes through Arctic waters for oil tankers which were not also ice-breakers. However, melting of parts of the Arctic ice cover is opening up coastal seaways which will make the transportation of oil out of the Arctic much easier, and would facilitate access to the oilfields in Alaska's National Wildlife Refuge. This was protected by law until the end of 2001, but there is increasing political and commercial pressure for these oilfields to be exploited. Oilfields off northern Russia are also likely to be exploited in the relatively near future. (Oil is already extracted from the continental shelf off the north coast of Alaska, the so-called North Slope, but that is carried south in the Alaska oil pipeline.)

Arctic ecosystems are also vulnerable to airborne pollution, particularly from industrial complexes in eastern and western Europe and the United States. Atmospheric conditions over the Arctic favour the condensation of pollutants such as PCBs, which tend to accumulate in body fats, particularly in top predators. Although these pollutants may be tolerated under normal conditions, they may be harmful if the animals are stressed and/or are mobilising fat reserves.

The term 'fragile Arctic', coined by the media, seems to suggest that Arctic ecosystems are more vulnerable to human interference and natural change than ecosystems in other parts of the globe. But is this true?

The food web shown in Figure 8.4 may look quite complicated, even though it has been simplified for the sake of clarity. However, compared with food webs in other regions, Arctic ecosystems, both marine and terrestrial, are simple, with a low diversity of species and relatively short food chains, i.e. few trophic levels.

- Why might a simple food web render an ecosystem more vulnerable?
- Because a problem with one link in the web – a temporary reduction in numbers, or an extinction – would have much more serious consequences than would be the case in a more complex system, where the animals have a wider choice of food species.

However, this view is not shared by all ecologists, some of whom argue that simple food webs are more robust than complex ones. Furthermore, although polar ecosystems involve relatively few animals, many of these animals are generalist feeders and do not depend on a single food resource, so this effectively means that there are more routes through the food web.

The way in which (say) pollution or environmental change affects populations of animals depends very much on the time-scale involved. Warm-blooded marine mammals and birds have relatively long lives – 50–100 years in the case of a killer whale, about 40 years in the case of an albatross.

- What implications do such long lives have for the survival of a population threatened by (say) a pollution incident?
- An individual pollution incident is likely to affect a region for (say) two or three years. For long-lived animals, several years with poor breeding success may have little effect on the number of young produced over a lifetime, and therefore little effect on the size of the population.

However, cold-blooded fish and invertebrates tend to have slow growth rates and low reproduction rates and (in comparison to mammals) relatively short lifetimes, so these can be badly affected by relatively short-term environmental changes. A series of relatively minor perturbations could prevent a species from recovering from a bad year, and events that elsewhere would be relatively unimportant could add up to an ecological catastrophe. Nevertheless, in high-latitude ecosystems, although diversity is low, numbers of individuals of a given species may be very large – think of krill and Arctic cod, for example – and this reduces the chance of a 'crash'. Also, Arctic and Antarctic ecosystems are both spread over large areas, so pollution damage to one region might be repaired by immigration of animals from adjacent regions.

Any widespread long-term decrease in numbers of fish or invertebrates would certainly have a serious impact upon the animals that feed on them, especially as the vulnerability of species tends to increase with evolutionary complexity (copepods, for example, are less vulnerable than fish). Most vulnerable of all are the marine mammals and birds, in which pollutants are in any case concentrated because they are at the top of the food web. If populations of top predators were to decline dramatically, the whole ecosystem would alter, both in terms of which species are dominant and in terms of the diversity of species overall.

All change in the Southern Ocean

As far as the Antarctic is concerned, the most-publicised impacts of global warming have been the breaking-off of large parts of the Antarctic ice-shelf, to form giant icebergs. Not so newsworthy is the fact that in parts of the Antarctic (particularly the waters around the Antarctic Peninsula) the winter sea-ice has not been persisting so long, and its extent has been decreasing i.e. the sea-ice extent shown in Figure 8.1d (formerly fairly typical for Antarctic sea-ice in winter) may not be typical of current and future decades. It is thought that this decline in the duration and extent of winter sea-ice may be responsible for the progressive decline in the abundance of Antarctic krill since the 1970s.

- Can you suggest why a decrease in the duration and extent of sea-ice might lead to a decline in krill numbers?

As shown in sequence 11 of 'Frozen Seas', during the winter months krill feed on algae living on the underside of sea-ice. Less sea-ice means less food for krill in winter, which could result in a decline in krill populations.

It is not simply that sea-ice provides a food-rich refuge where krill can survive the winter, but also that well-fed adult krill are more likely to reproduce successfully later in the year. A long duration, and wide extent, of sea-ice cover correlate with an early onset of the krill spawning season in spring/summer and good breeding success for the krill, with high survival rates for the juveniles. (As alluded to in 'Frozen Seas' (sequence 11), after spawning, krill revert to a juvenile stage, thus saving energy while overwintering under the ice.)

The decline in krill populations is part of wider change in the ecosystem of the Southern Ocean, being brought about by global warming. An ecosystem in which krill play the pivotal role seems to be changing into one in which gelatinous species – in particular, salps – are dominant; salps are the barrel-shaped 'jellies' shown in sequence 5 of 'Open Ocean', and are characteristic of low-nutrient areas. After winters of limited sea-ice cover, there are early phytoplankton blooms in the open water around Antarctica, allowing the salp populations to explode. Salps typically live in warmer water than krill, and it had been assumed that such species would not take hold at high southern latitudes because of the extremely low water temperatures; however, global warming seems to be tipping the balance in favour of salps rather than krill. You might like to consider what implications a greatly decreased krill population might have for the other animals of the Southern Ocean.

A marked reorganisation of an ecosystem from one relatively stable state to another is known as a *regime shift*. In Chapter 11, you will see how comparable ecological changes in northern waters are having a serious impact on fish populations.

Migrations

9

The Blue Planet programmes contain various sequences that relate to migrations of marine animals. In some ways, the migrations are very different from one another but, as you will see, they also share certain features in common.

9.1 Whale migrations

The Blue Planet introductory programme begins with a magnificent blue whale feeding on krill, probably in Arctic waters. Most of the great baleen whales spend part of the year feeding at high latitudes – around the melting Arctic pack-ice and between the Arctic islands, and along the retreating ice-edge in the Southern Ocean (Section 8.2) – and spend the rest of the year in warmer waters where food is more scarce. During the short polar summer, the great baleen whales probably eat about 3–4% of their body weight each day, which in the case of a blue whale amounts to 2–2.5 tonnes of krill. Then, having increased their body weight by perhaps 50–70%, they travel several thousand kilometres to live where there is about a tenth of the food, and they will lose so much weight that by the time they return to their summer feeding grounds their blubber store will be largely used up. Why do they undertake these marathon migrations?

The simple answer is: to breed. But why do they not breed in polar waters in summer, like their smaller toothed relations, beluga and narwhal? Or indeed, like the polar pinnipeds?

One reason could relate to the availability of their respective food supplies.

- Can you suggest what this might be?
- Plankton – the main food of the baleen whales – are only abundant in high-latitude seas for a few months each year, whereas fish – the food of most of the carnivorous toothed whales – are available all year round.

However, this cannot be the whole answer. For one thing, some toothed whales also make quite short summer visits to polar regions. One possibility is that the time spent at lower latitudes is a legacy from the distant past when climatic patterns were different and tropical regions were more biologically productive than they are now. This idea is supported by the fact that fossil remains of the earliest baleen whales have only been found at low latitudes.

It also seems likely that baleen whales do not stay all year at high latitudes because newly born calves do not have sufficient blubber to insulate them from cold polar waters, and so need to be weaned in warmer waters. Also, it is possible that, because the suckling calf has to make such an enormous amount of growth, the food required by the mother cannot be consumed in the short period of high productivity of the polar summer.

- What lower-latitude regions would you expect to be favoured by plankton-feeding whales, including those which have migrated from high latitudes after the polar summer?
- Upwelling areas (cf. Figure 5.11c), notably the Equatorial Divergence and eastern coastlines affected by the Trade Winds.

Perhaps the best-known whale migration routes are those of the gray whale, which of all the baleen whales is the one that lives closest to shore, and is often seen within a kilometre of the coast. There are two populations of gray whales, one with winter calving grounds in the shallow lagoons of Baja California and another with winter calving grounds off Korea and around Japan. Each spring, the Californian 'grays' are watched by thousands of people as they travel north along the coast of North America *en route* to the Bering Sea and Chukchi Sea to the north of the Bering Straits, and then again in the autumn as they travel back to Baja California. Meanwhile, similar migrations are taking place along the margin of the western Pacific, to and from the same summer feeding grounds.

Migration patterns are not as simple as we may have suggested, and vary between species and between the same species in the Northern and Southern Hemisphere. For example, not all baleen whales travel to low latitudes to breed. One population of bowhead whales winters in the Bering Sea (between Alaska and Siberia), where the calves are born, and in summer they follow the leads in the pack ice to the Beaufort Sea (off northern Alaska). Another population of bowheads winters and calves in the Labrador Sea, and in summer travels to coastal inlets around Baffin Island.

Some toothed whales also migrate. In the case of sperm whales, females and juveniles usually remain in tropical and subtropical waters, while the males travel from low latitudes to the polar regions. This could be partly because the young have insufficient blubber for polar waters and need protection from their mothers, and partly because the males can avoid competing with their calves for food resources by feeding elsewhere. (Also, some populations of squid, on which sperm whales feed, may themselves be migratory.)

Dolphins and other small whales make seasonal migrations in search of food, either moving onshore and offshore, or visiting particular sites where productivity is high at certain times of year. The dolphins and pilot whales heading off to the Azores at the end of 'Open Ocean' are on such a migration.

On the basis of what you have just been reading, can you explain why, if whales shift their migration routes in response to noise pollution (as discussed in Section 8.4.3), it could have negative effects on the health of the whale population concerned?

Migration routes need to be as efficient as possible, so that the amount of energy used in travelling to and from the feeding grounds can be at least compensated for by the energy provided by the food consumed while at the feeding ground. If the journey to and from the feeding ground is too long, the whales will become undernourished. Female whales in poor condition are likely to produce less viable young when they return to the calving grounds.

Whales may die of starvation, particularly when on migration.

9.2 Fish migrations

As far as fish are concerned, environments that are good for spawning (i.e. producing eggs) are very often not good for young to grow up in, nor for adults to feed in, and many marine fish species have a migratory cycle which allows each stage to prosper, and so maximises reproductive success. For example, North Sea plaice (*Pleuronectes platessa*) spawn in the very south-western part of the North Sea, and the young – which are members of the meroplankton (Section 4.4) – are carried in currents to the

sheltered waters of the Wadden Sea (off the Netherlands and western Germany). This journey between the spawning ground and the nursery areas is the most hazardous period of their lives. It is timed to coincide with the spring phytoplankton bloom, but if weather conditions result in the bloom being late, the peak in zooplankton numbers, on which the larvae feed, will also be late, and the young plaice will starve to death before they reach the Wadden Sea. If they do not starve, they may well be eaten.

After about five weeks as larvae, the young plaice metamorphose into tiny versions of the adult fish and descend to the sea-bed as they are carried by currents to their nursery areas. After spending a year or more in the Wadden Sea, the young plaice swim to the northern part of the North Sea, where they feed until the time arrives to spawn.

Thinking back to Section 3.4 (Hitching a ride on the tide), can you recall how demersal fish like plaice save energy during their migrations?

They swim with the current when the tidal current is flowing in the direction they are travelling in, and rest on the bottom during the other half of the tidal cycle.

Herring (*Clupea harengus*) in the North Sea spawn off eastern Scotland and the larvae drift shorewards. Then, as the young adults grow they move eastwards into deeper water, with the main feeding grounds being off Norway. The herring of the Pacific make similar migrations – you may remember the baby herring in the feeding grounds off Vancouver Island in 'Seasonal Seas' (sequence 11).

This type of migratory pattern, with separate spawning grounds, nursery grounds and adult feeding grounds, is adopted by a wide variety of nektonic species – fish, squid and even large crustaceans. Even for strong swimmers – tuna, for example – the migration routes make use of the prevailing currents. The young yellowfin tuna, seen in 'Open Ocean' (sequences 1, 3 and 7), were carried as larvae to the western Pacific in the westward-flowing currents of the equatorial current system (Figure 5.2).

In the case of animals that live on or near the bottom (like the plaice), whose eggs rise to the surface to become part of the plankton, and develop into planktonic larval animals, the migration has a vertical dimension. Indeed, this is true of all animals that produce meroplankton (as seen in 'Seasonal Seas', sequence 8). There are other animals that migrate into shallower coastal waters to mate, and lay their eggs there – an extreme example of this behaviour is provided by the capelin, seen in the introductory programme – and yet others which swim up to the surface to mate, and then return to deeper water to lay their eggs. The spectacular firefly squid, which you will see in part II of 'The Deep', is one such animal.

As mentioned in Chapter 3, many estuarine invertebrates and fish travel between seawater and freshwater as part of their reproductive cycles.

Can you give any examples of (1) fish which spend most of their time in the sea, but spawn in freshwater, and (2) fish which spend most of their lives in freshwater, but spawn in the sea?

The best-known examples are probably (1) salmon, and (2) freshwater eels.

Other sea fish which breed in freshwater – i.e. *anadromous fish* – are the shad and the sea lamprey. Freshwater fish which spawn at sea, including eels of the genus *Anguilla*, are described as *catadromous*. All these fish are relatively primitive, and some biologists believe that their migrations are somehow a hangover from a time when these fish lived in shallow brackish water, in estuaries and along coasts.

However, in the case of eels, the migrations are very long indeed. As far as North Atlantic populations are concerned, there are two species of eel, both of which spawn in the Sargasso Sea, the centre of the North Atlantic subtropical gyre, to the east of the Gulf Stream (Figure 5.10). *Anguilla anguilla* (the European eel) spends most of its adult life in rivers, streams and estuaries in Europe, and *Anguilla rostrata* (the American eel) similarly spends most of its adult life in North American freshwaters.

Question 9.1 Thinking back to Figure 2.5, can you suggest a possible origin for these long migration routes from the mainland (especially the European mainland) to the Sargasso Sea? ◀

The ancient distribution of continents could also help to explain why green turtles that live and feed off the coast of Brazil swim 2000 km to breed on Ascension Island in mid-Atlantic (as shown in sequence 7 of the introductory programme). However, it does little to explain why leatherback turtles, that are regularly seen feeding on jellyfish and salps in the north-eastern Atlantic, breed on beaches along the coast of Brazil.

9.3 Vertical migration

Every evening at dusk, over large parts of the oceans, there is a mass migration of marine animals up towards the surface; every morning, around dawn, the animals begin to return to the depths ('Open Ocean', sequence 3). This amazing phenomenon has been known about for nearly 200 years, but we still do not have an entirely satisfactory explanation for its ecological significance. It is sometimes known as 'diurnal migration', but as diurnal means 'pertaining to the day' (i.e. is the opposite of 'nocturnal'), this behaviour is more properly known as *diel* migration, meaning migration 'once a day' or 'every 24 hours'.

Vertical migration began to be brought to the attention of marine scientists with the widespread use of sonar (i.e. echo-sounding) for bathymetric measurements in the 1950s and 1960s. Sonar traces often show 'deep scattering layers', sound-reflecting layers *within* the water column that look similar to reflections from the sea-bed. Admiralty charts produced in the 1950s therefore included a number of non-existent 'shoals' (i.e. shallow areas), and it was only when it was realised that these layers moved with a 24-hour rhythm that animal behaviour began to be suspected. As many as five different layers can be distinguished on a single echo-sounder record, between depths of about 100 m and 1000 m. These may be caused by gatherings of larger crustaceans (e.g. krill and shrimp), small fish with sound-reflecting swimbladders (e.g. lanternfish), and even large copepods. To some extent, the layers may be artefacts of the fact that for some animals (especially fish with swimbladders) the strength of the echo changes with the pressure the animal is under, so that an echo-sounder can only 'see' the animal over a certain depth range.

At night, the distinct layers are observed to rise to the surface and become diffuse or merge into a broad band extending down to about 150 m. Diel migrations are tuned to the light–dark cycle, and the depth zones occupied by different species are influenced by daylength, as well as factors like cloud cover, or even bright moonlight and eclipses.

The vertical distance travelled over 24 hours varies, with larger species and better swimmers generally travelling further. However, even small copepods will travel several hundred metres twice a day. Copepods and the larvae of barnacles and crabs

can swim upwards at 10–170 m per hour, with larger crustaceans (e.g. krill), which can swim at 100–200 m per hour, making a twice-daily journey of 800 m or more.

What possible advantages could there be for zooplankton to migrate in this way? Consider for a while, and try to come up with some suggestions.

Many hypotheses have been advanced to explain vertical migrations. Here are three:

1 Food is more abundant in the sunlit surface layers, but this is also where animals are most vulnerable to predators which hunt by sight. One solution to this might be to hide at depth by day, in darkness or near-darkness, and only rise to the surface to feed at night. The fact that many migrants are transparent, or very small, suggests that the animals that prey on them do hunt by sight.

2 Another possibility is that zooplankton conserve energy by spending non-feeding time in colder, deeper water. As you know, metabolic rates are lower in colder conditions (Section 2.1.2), and it has been shown that the amount of energy saved by spending part of the day in a colder environment offsets the energy used in migrating (though both are only a few per cent of metabolic energy).

3 Another hypothesis is that because water at different depths moves at different speeds, and sometimes in different directions, migrating animals can feed in different bodies of water without having to travel horizontally. For example, they could be in plankton-poor waters one night, but when they come to the surface the next evening could well find themselves in a different, more nutrient-rich body of surface water, with more phytoplankton. This could also prevent them overgrazing a particular patch of productive water.

The most likely explanation is the first one, but it is possible that all of these hypotheses are correct, with different factors being more or less important depending on the circumstances. It seems that the migration of zooplankton is the incentive for the vertical migration of other larger animals, including fish and squid. Some of these may migrate from a depth of 1000 m – the record is held by a lanternfish (*Ceratoscopelus warmingeri*) living off the Azores, which migrates through about 1600 m, taking three hours to make the journey each way.

Whatever the underlying reason, the phenomenon itself, filmed so that small organisms can be seen clearly, is spectacularly beautiful. You might like to take this opportunity to look at sequence 6 in part II of the 'The Deep', which shows different vertically migrating animals from those in sequence 3 of 'Open Ocean'.

Question 9.2

What *two words* could be used to summarise the reasons why animals in the ocean undertake migrations? ◀

10 The deep ocean

So far in this book, we have been looking mainly at life in shallow seas and in the uppermost layers of the open oceans. Our knowledge of these relatively accessible waters has grown enormously over the past half-century; by contrast, our knowledge of the deep ocean and the deep sea-floor – the largest living spaces on Earth (cf. Figures 2.4 and 2.7) – is still little better than our knowledge of the surface of the Moon. However, since the 1950s, and particularly over the past 5–10 years, technological advances have allowed us to learn more about the deep sea through investigations using manned submersibles (submarines designed to travel mainly up and down in the ocean, rather than horizontally; Figure 10.1); through the deployment of 'landers' (frames supporting instruments, samplers and cameras, which are deposited on the sea-floor, and left there for days, weeks or even months); through photographs taken from camera 'sleds' that are towed above the sea-bed; and, increasingly, through the use of remotely operated vehicles (ROVs). However, the volume of deep ocean, and the area of deep sea-floor, that has been studied in this way is minute compared with the total deep 'living space' – less than 0.001% of the area of the abyssal plains has been explored (i.e. 1000 times *less* than the 1% mentioned in 'The Deep').

Ideas about life in the deep sea have changed dramatically over the last two centuries, so here we are taking a slightly different approach to that in previous chapters, by adopting an historical perspective.

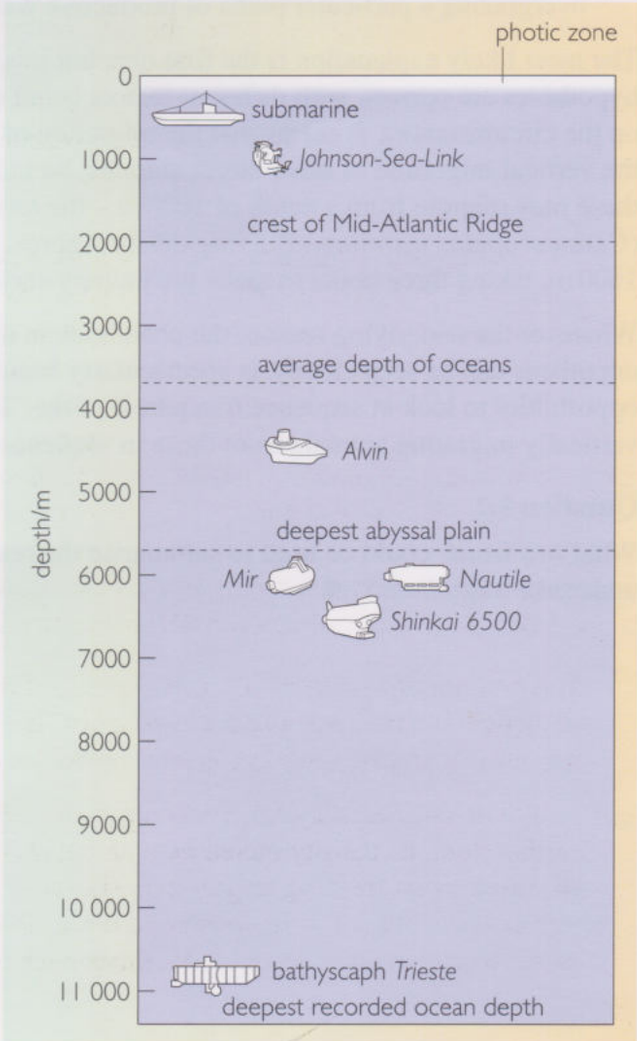


Figure 10.1 Schematic diagram to show the depth capabilities of various submersibles in relation to the depths of certain oceanic features. *Alvin*, perhaps the best-known submersible, can descend to a depth of 4500 m; *Johnson-Sea-Link* can dive to 1000 m (both *Alvin* and *Johnson-Sea-Link* appear in 'The Deep', and are American). The Russian submersible *Mir* and the French *Nautile* have both descended to 6000 m, but the depth record is held by the Japanese submersible *Shinkai 6500*, which has descended to 6526 m, in the Japan Trench. The first successful 'untethered' vehicle was August Piccard's *Trieste*, launched in 1953. It worked on the same principle as a balloon: it sank because of several tonnes of ballast, which was detached when the time came to ascend. In 1960, the *Trieste* descended 11 000 m into the Challenger Deep in the Marianas Trench (Figure 2.5), the Challenger Deep remains the deepest known feature on the face of the Earth.

10.1 Life in the deep sea: an historical perspective

Watching the Blue Planet programmes, particularly 'The Deep', it is hard to believe that up until the middle of the 19th century it was a generally accepted 'truth' that below a certain depth the ocean was totally devoid of life. This idea, known as the 'azoic theory', persisted long after there was abundant evidence to the contrary.

There were a number of reasons why the 'azoic theory' was so persistent. In the first place, it had been put forward in the 1840s by a very respected scientist, Edward Forbes, and so was not really questioned or investigated further, even though it was based on rather limited evidence. As early as 1818, an expedition in search of the North-West Passage through the Arctic had brought up deep-sea organisms, but communication between scientists and surveyors, hydrographers and explorers (who were responsible for much of the oceanographic work of the time) was poor. Unfortunately, at a time when specialisation was becoming intense, there was little communication among specialists in the various branches of science. Furthermore, there seemed little point in devoting resources to investigating the deep sea, when it was taken for granted that everything of interest or commercial value (fish, whales, etc.) was to be found in surface or shallow waters.

In addition to these social and practical difficulties, there were scientific impediments to an improved understanding of the deep ocean, and beliefs about the deep-sea environment supported the assumption that conditions there were inimical to life. Let's look briefly at how received wisdom about temperature, seawater density, circulation within the ocean, and pressure, all conspired (apparently) to confirm the idea that the deep ocean was a lifeless abyss.

Temperature

It was (and often still is) generally assumed that seawater behaves like freshwater, freezing at 0 °C and attaining its greatest density at 4 °C (lower curve in Figure 10.2). As a result of this assumption, people imagined that in winter at high latitudes, surface water would cool until it reached 4 °C, at which point it would be denser than underlying water (unless that were also at 4 °C) and so would sink. In doing so, it would displace less dense water, which would rise to the surface and be cooled in turn, until it, too, sank at 4 °C. Over millennia, the deep ocean would thus fill up with water at 4 °C. Even when surface temperatures were lower than this, the deep reservoir of still water would be unaffected, and would become stagnant; given the continual 'rain' of dead and decaying organisms, it would become devoid of oxygen, and would thus be unable to sustain life.

- At first sight, this scenario of a deep stagnant reservoir seems a reasonable deduction. On the basis of your reading of Section 2.1.1, and the upper curve in Figure 10.2, can you explain why the reasoning is flawed?
- Unlike freshwater, seawater cools down to −1.9 °C before freezing. Furthermore, its density increases with decreasing temperature and is at a maximum at its freezing temperature (i.e. at −1.9 °C). This means that under very cold conditions, water cooled at the surface can become sufficiently dense to sink to great depths, sometimes even to the deep sea-bed.

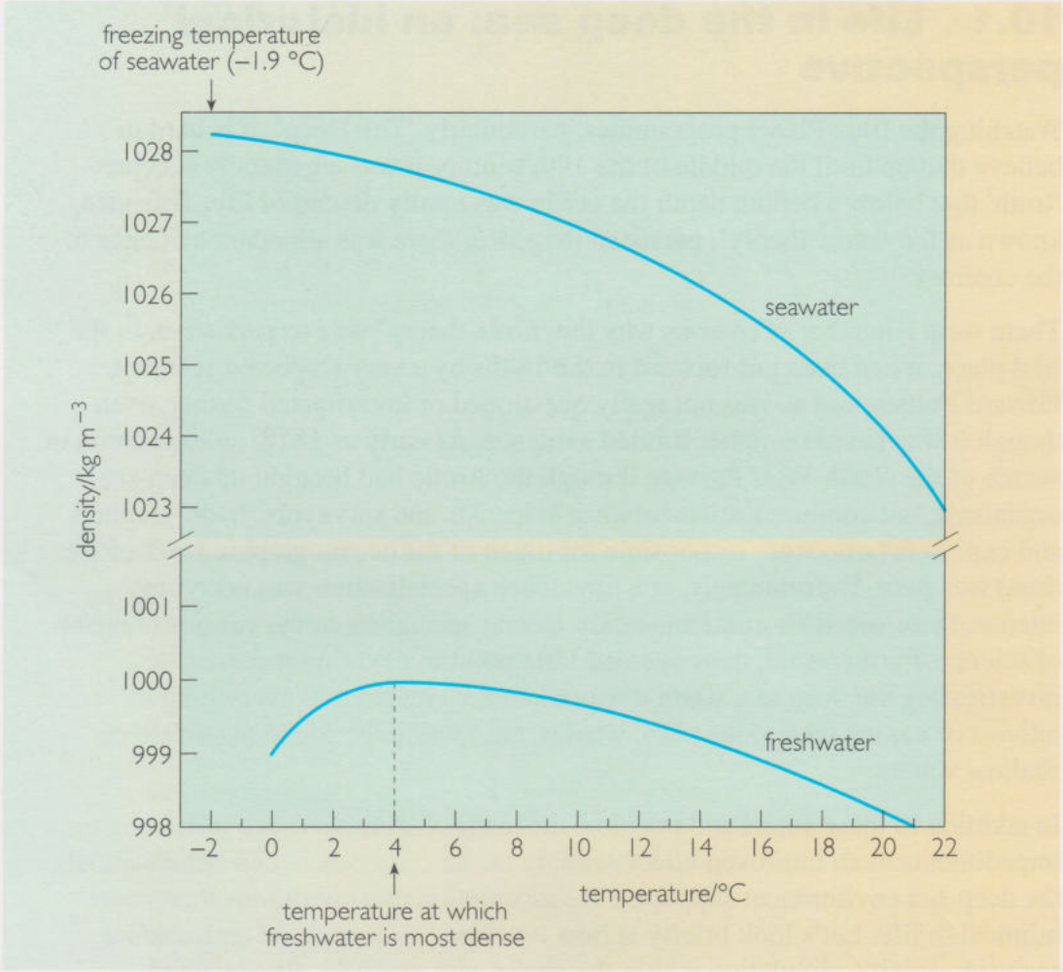


Figure 10.2 Graph showing the variation with temperature of the density of freshwater (lower curve) and seawater of average salinity (35) (upper curve).

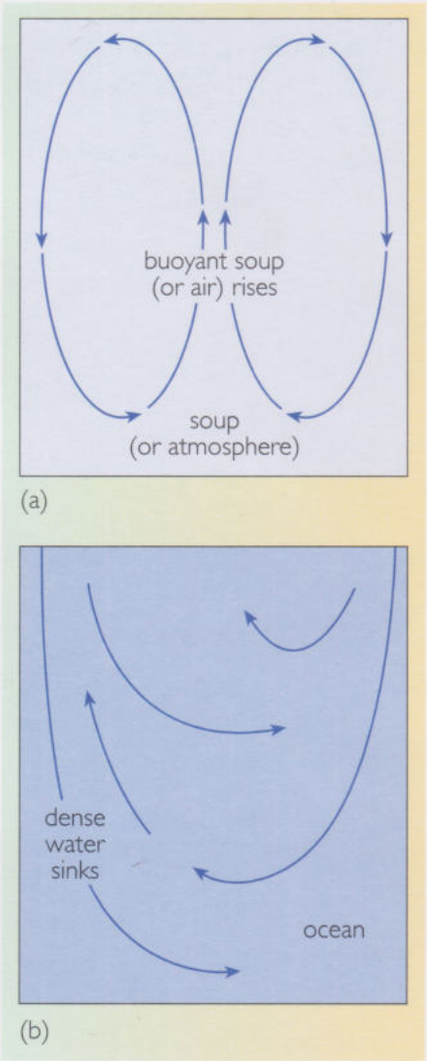


Figure 10.3 The difference between convection in (a) a pan of soup or the atmosphere, and (b) the ocean.

The deep 'vertical' circulation in the ocean is a kind of convection. The type of convection with which we are most familiar is where a liquid (or more strictly fluid, i.e. a gas or a liquid) is warmed from beneath and rises: as everyone knows, 'warm air rises'. What we really mean is 'air that has become warmer than its surroundings (and hence *less dense* than its surroundings)' rises. If we heat a pan of soup on a ring, the warmed soup at the bottom expands and so becomes less dense. It rises to the surface, displacing colder soup, which sinks downwards, becoming warmed in turn (Figure 10.3a). In the case of the ocean, convection occurs as a result of *cooling from above*, so that surface water increases in density and sinks (Figure 10.3b). How far it sinks depends on its density relative to the density of the water through which it is sinking. It is not possible for water of higher density to overlie water of lower density for any length of time – this is an unstable situation, and will result in the water column 'turning over'. In other words, the normal situation in the ocean is that, at any one location, the density of seawater increases with depth, from the surface layers to the deep sea-floor.

Figure 10.4 shows in broad terms what we now know about the vertical temperature distribution in the Atlantic Ocean; the lines joining points of equal temperature are known as *isotherms*. For the sake of simplicity, in mid- and low latitudes the 10 °C isotherm is shown as marking the lower limit of the warm water above the permanent thermocline (the depth zone within which temperatures decline to about 4 °C; cf. profiles in Figure 4.9); at high latitudes, strong winter mixing means that temperatures are fairly similar at all depths. Superimposed on the temperature distribution in Figure 10.4 is the large-scale pattern of north–south (or 'meridional') current flow below the surface layer, which gives rise to this temperature distribution.

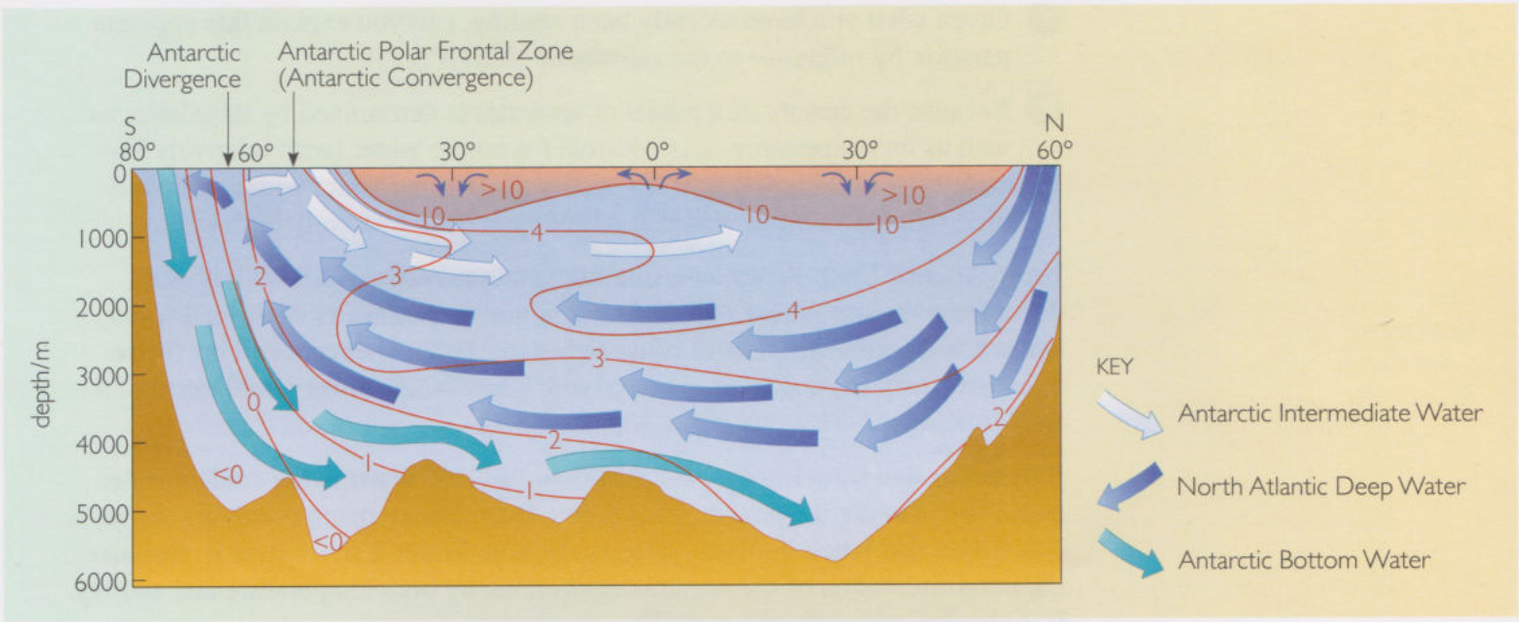


Figure 10.4 Generalised north–south cross-section of the Atlantic Ocean between 80° S and 60° N, showing the distribution of temperature, and the main features of the deep circulation. At the Antarctic Polar Frontal Zone, Antarctic surface waters flowing north converge with warmer subtropical waters and sink beneath them; at the Antarctic Divergence, water that sank at high northern latitudes eventually reaches the surface again. Small downward arrows near the surface at about 30° latitude represent convergence in the subtropical gyres (Figure 5.6a), and small upward arrows near the surface at the Equator represent upwelling at the Equatorial Divergence (cf. Figure 5.5). *Note* The vertical scale is greatly exaggerated; temperatures on isotherms are in °C.

It is important to remember that the circulatory pattern within the body of the ocean (i.e. in the vertical plane) is determined by processes occurring *at the surface*. At divergences, surface waters driven apart as a result of wind patterns are replaced by water welling up from below; at convergences, surface waters come together and may sink (Section 5.2.1). Furthermore, the temperature of a parcel of water within the body of the ocean will have been determined when it was at the surface, through a combination of warming by solar radiation and cooling by winds.

Thinking back to Section 2.1, can you suggest another characteristic property of seawater that is determined by processes occurring at the sea-surface?

The property is salinity – the total concentration of dissolved salts. This is increased by evaporation from surface waters, and decreased by precipitation.

Water that sinks from the sea-surface under particular climatic conditions acquires a characteristic combination of temperature and salinity, and is identified as a particular *water mass*. The body of water that is formed by sinking at the Antarctic Polar Frontal Zone is known as Antarctic Intermediate Water (AAIW). Precipitation is high in subpolar regions (as atmospheric pressure tends to be low; Figure 5.1) and this, together with the addition of large amounts of meltwater, means that AAIW is relatively fresh (for seawater).

If you look at the temperature distribution on Figure 10.4, you can see that between about 40° S and the Equator, the isotherms form a kind of 'tongue', corresponding to the northward spread of AAIW, centred on a depth of about 1000 m. This spreading AAIW is *colder* than both the water above *and* the water below, which is known as North Atlantic Deep Water (NADW). At first sight this may seem an impossible situation, given that, for stability, density must increase with depth everywhere in the ocean.

Given what you have recently been reading, can you explain this apparent paradox by reference to the salinity of NADW?

Because the density of a parcel of seawater is determined by its salinity as well as its temperature, it is possible for cooler water (with relatively low salinity) – in this case, AAIW – to overlie warmer water with a relatively high salinity. In other words, NADW must have relatively high salinity.

North Atlantic Deep Water and Antarctic Bottom Water (AABW) both sink down from regions where sea-ice forms in winter. Sea-ice is itself freshwater, and when it forms, droplets of brine-rich water collect beneath it. This 'brine-rejection' (as it is known), into underlying water which is very cold, results in the formation of dense water masses.

As you can see from Figure 10.4, Antarctic Bottom Water is the coldest water mass, and also the densest; North Atlantic Deep Water, being relatively warm, is less dense, and when it meets Antarctic Bottom Water it flows over it. Because the deep circulation of the ocean is determined by both temperature and salinity, it is also known as the *thermohaline circulation*.

So, the deep ocean is filled with generally slow-moving water of varying temperatures and salinities, *not* by a still pool of water at 4 °C. What is more, this water is well oxygenated, because it has sunk down from the surface where it was in contact with the atmosphere, and air bubbles were churned down into it.

Thinking back to Sections 1.4 and 4.5, can you suggest another reason why surface waters are well oxygenated?

Photosynthesis of phytoplankton living in the photic zone produces oxygen as a by-product (Equations 1.1a and 4.1), and this dissolves in the surrounding water.

As water sinks down away from the surface layer, the oxygen it contains is used in respiration by living marine organisms (from plankton to whales) and by bacteria bringing about the decomposition of dead organisms (Section 4.5). Furthermore, once it is below the photic zone, no more oxygen can be added to the seawater. Nevertheless, below about 1000 m depth, concentrations of dissolved oxygen begin to increase again.

Given what you know about the solubility of gas in water (Section 2.1), can you explain how the flow pattern shown in Figure 10.4 gives rise to this increase in dissolved oxygen below 1000 m?

Deep water masses are very cold. As discussed in the Notes for 'Tidal Seas' (sequence 17), and in Section 4.5, cold water can contain more dissolved gas than warm water. Water in surface layers at high latitudes can therefore contain more dissolved oxygen than surface waters at lower latitudes. As a result, when deep water masses such as NADW and AABW sink and flow equatorwards (Figure 10.4), they carry large amounts of oxygen down into the body of the deep ocean and down to the deep sea-bed.

Because deep water masses are well oxygenated, they are often described as 'ventilating' the deep ocean.

Pressure

In the 1870s, Charles Wyville Thomson, one of the first naturalists to investigate the biology of the deep sea, wrote:

> The enormous pressure at these great depths seemed at first sight alone sufficient to put any idea of life out of the question. There was a curious popular notion, in which I well remember sharing, when a boy, that in going down, the seawater became gradually under the pressure heavier and heavier, and that all the loose things in the sea floated at different levels, according to their specific weight: skeletons of men, anchors and shot and cannon, and last of all the broad gold pieces wrecked in the loss of many a galleon on the Spanish Main; the whole forming a kind of 'false bottom' to the ocean, beneath which there lay all the depth of clear still water, which was heavier than molten gold. *The Depths of the Sea* (1873)

These romantic ideas stemmed not so much from a misunderstanding of the effect of pressure, but from an assumption that seawater was much more compressible than it actually is.

The pressure at depth in the ocean is the force resulting from the overlying weight of water. As Wyville Thomson put it: At 2800 fathoms (~3700 m) 'a man would bear upon his body a weight equal to twenty locomotive engines, each with a load of pig iron'. Unlike some of his contemporaries, he realised this great pressure would not preclude life in the deep sea, any more than the pressure of the atmosphere precludes it on land, because a deep-sea organism is 'supported through all its tissues on all sides … by incompressible fluids at the same pressure'. In other words, as the tissues of deep-sea organisms are filled with fluid, and the pressure inside is the same as that outside, they are in no danger of being crushed by the overlying water. By the same token, a water-filled ball released from a submersible at a depth of several thousand metres would merely be slightly compressed (as water is slightly compressible), although a hollow ball would be crushed to a fraction of its size.

The pressure at a given depth in the ocean is the weight of the overlying water (plus the weight of the overlying atmosphere, which is negligible by comparison).

- Given that the bulk of water below the thermocline is between 2 and 4 °C (Figure 10.4), what is the average density of the bulk of ocean water below the thermocline? (Use the appropriate curve in Figure 10.2, and make an *estimate* only.)

- Lines drawn up from 2 and 4 on the horizontal axis of Figure 10.2 intersect the 'seawater' curve at points corresponding to density values of about 1027.75 and 1028. This means that the density of seawater (assuming an average salinity of 35) is generally between 1027.75 kg m^{-3} and 1028 kg m^{-3}.

In other words, a cubic metre of seawater has a mass of about 1030 kg, or just over 1000 kg. As it happens, this means that for every 10 m increase in depth in the ocean, the pressure due to the weight of overlying water (hydrostatic pressure) increases by an amount equal to the pressure exerted by the atmosphere, also known as 1 *bar* (after the Greek for 'weight'). Oceanographic equipment (e.g. for recording temperature profiles like those in Figure 4.9) is often calibrated in decibars (1 dbar = 0.1 bar) because of the useful correspondence between decibars and metres; and, as you are probably aware, meteorologists commonly use millibars (cf. Section 3.6). However, we should mention for completeness that the SI unit for pressure is the pascal (Pa).

Question 10.1 What is the pressure (in decibars) at the bottom of the Challenger Deep, in the Marianas Trench? (*Hint:* Look at Figure 10.1.) ◀

As Figure 10.4 illustrates, water masses occupy enormous volumes of ocean. This means that below the permanent thermocline, temperature is more or less constant over large horizontal distances, or at least it changes only very gradually; the same is true of salinity and (to a lesser extent) oxygen concentrations. Because environmental conditions at a given depth are so similar over such large ranges, so are the communities of animals living in those waters. Some deep-water planktonic and pelagic species are found in all three of the Atlantic, Pacific and Indian Oceans; others have a more limited distribution.

Figure 10.4 also shows that enormous areas of sea-bed are overlain by the same water masses (and AABW is found in all three oceans). The communities of animals living on the abyssal plains – the most extensive environments on Earth (Section 2.3) – are therefore also similar over great areas, though there are differences between the three oceans.

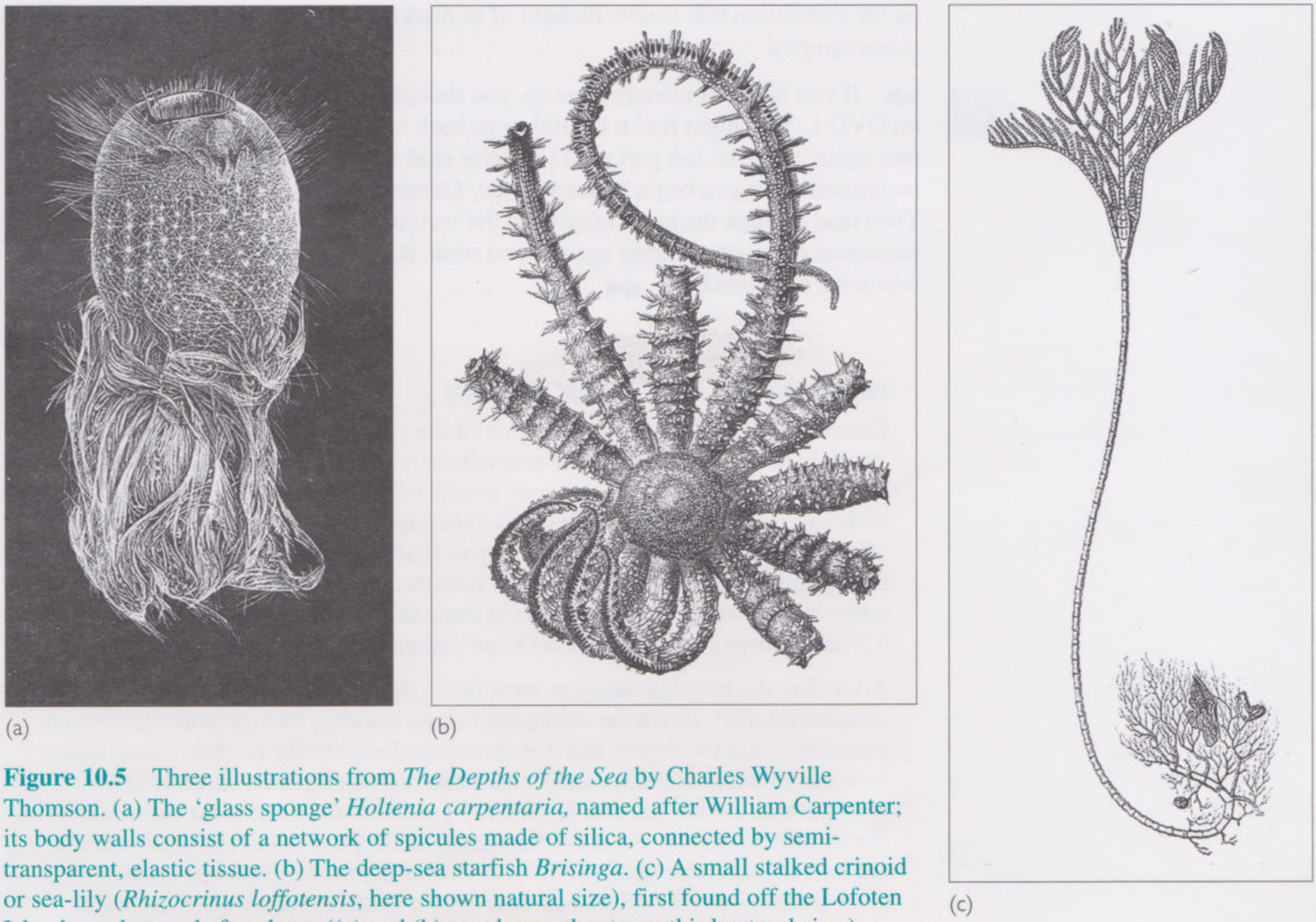
- Bearing in mind the topography of the deep sea-floor (Figures 2.4 and 2.7), would you expect communities of sea-bed animals found in the western Atlantic to be the same as those found in the eastern Atlantic, or those in the western Pacific to be the same as those in the eastern Pacific?
- No, because the Mid-Atlantic Ridge and the East Pacific Rise act as topographic barriers, which hinder the spread of species and keep populations apart.

While the species making up sea-bed communities change almost imperceptibly across the abyssal plains, there are marked changes in communities with increasing depth down the continental margin. The reasons for this are not fully understood, but pressure may play an important role in determining which species thrive over which depth ranges.

The voyages of the Lightning *and the* Porcupine

Having discussed ideas about the effects of pressure in the deep sea by reference to Wyville Thomson, we should end this section by a brief look at his later great achievements in deep-sea marine biology. Early in his career, Wyville Thomson had worked with Forbes, and for many years he accepted the azoic theory without question. By the mid-1860s, however, he had become convinced that the theory was untenable; indeed he had begun to see the deep sea as 'the land of promise for the naturalist'.

In 1868, together with friend and colleague William Carpenter, Wyville Thomson set out on an expedition to study the marine life of the deep waters and sea-bed to the north and north-west of the Scottish Western Isles. Here, beyond the continental shelf (cf. the 200 m depth contour in Figure 3.4), depths become well in excess of 1000 m. The Royal Navy made available the rather decrepit HMS *Lightning*, and although she was barely seaworthy, the expedition was a great success from the scientific point of view; four more deep-water cruises followed, in the sturdier HMS *Porcupine*. The discoveries made during the cruises of the *Lightning* and the *Porcupine* were recorded in scientific reports, but it was thought that they should also be made available to the general public. The account that Wyville Thomson compiled was published in 1873, entitled *The Depths of the Sea*. It was an erudite and comprehensive discussion of discoveries and ideas, and was regarded by many as a literary masterpiece.



(a) (b) (c)

Figure 10.5 Three illustrations from *The Depths of the Sea* by Charles Wyville Thomson. (a) The 'glass sponge' *Holtenia carpentaria,* named after William Carpenter; its body walls consist of a network of spicules made of silica, connected by semi-transparent, elastic tissue. (b) The deep-sea starfish *Brisinga*. (c) A small stalked crinoid or sea-lily (*Rhizocrinus loffotensis*, here shown natural size), first found off the Lofoten Islands, and named after them. ((a) and (b) are shown about one-third natural size.)

Figure 10.5 shows three of the illustrations from *The Depths of the Sea*. Echinoderms, especially crinoids (the most primitive of the echinoderms), were a particular interest of both Wyville Thomson and Carpenter. They were familiar with featherstars, but knew stalked crinoids or sea-lilies only from fossils (cf. Sections 1.1 and 1.2). However, in 1867 Wyville Thomson was shown a small sea-lily (Figure 10.5c) by an eminent Norwegian colleague, who had dredged it up from a depth of 600 m. This exciting discovery occurred only nine years after publication of Charles Darwin's *Origin of Species*, and it encouraged Wyville Thomson in his belief that ancient animal forms, or 'living fossils', could be found in the deep sea – indeed, this had been one of the incentives for the deep-water cruises. Wyville Thomson believed that 'living fossils' were most likely to be found in the deep sea, because the 'main cause of the destruction, the migration, and the extreme modification of Animal types, appears to be change of climate', which (he said) only affects the Earth's surface and upper part of the ocean. We will come back to this idea at the end of the chapter.

The deep-water cruises of the *Lightning* and the *Porcupine* put Britain at the forefront of marine science, but within a few years other countries had begun to catch up. Carpenter felt that the scientific techniques developed on the Atlantic cruises of the *Lightning* and the *Porcupine* should be put to use in other oceans, and he campaigned for a government-sponsored scientific circumnavigation of the globe. By 1872, Carpenter's idea had become a reality, and HMS *Challenger* set out from Portsmouth

on the expedition that is now thought of as marking the birth of modern oceanography.

▶▶ If you have not already done so, you should now look at part II of 'The Deep' on DVD 1. You might find it helpful to go back to the beginning and watch the first part again. Save the last part until you have read Sections 10.2 and 10.3. We recommend that you begin by reading the 'General note' and then watch all of part II. Then read through the notes relating to the various sequences, and play those sequences (or parts of them) again if you wish. Read the 'Activities' paragraph whenever suits you best. ◀◀

Notes on the 'The Deep' (part II)

General note Whereas the first part of the 'The Deep' was about the 'twilight zone', for much of the second part we are seeing animals that normally live in complete darkness, except when they are illuminated by bioluminescence (or the lamps of a submersible). However, about 11 minutes 20 seconds in, there is an excursion up to shallower depths with the mating firefly squid (sequence 5), and this is followed by a sequence about the large-scale vertical migration that occurs at dusk and dawn, as described in Section 9.3 (and shown briefly in 'Open Ocean', sequence 3).

After that, the storyline takes us back down into the depths, along the continental shelf, down the continental slope and rise, and out onto the abyssal plain (note that the depths and distances mentioned in the narration vary from location to location and are not as hard and fast as might be suggested). Just after the start of the 'journey to the very bottom of the deep sea' (sequence 7), the narration says 'At around 300 metres, the drop-off levels out and we move out onto the continental slope.' If you look at Figure 2.7, you will see that this must actually refer to the change in sea-floor gradient where the continental slope gives way to the more gently sloping continental rise. (The angle of the camera seems to be exaggerating the slope of the sea-bed in these shots; as discussed in Section 2.2, the gradient of the continental slope is typically about 1 in 20, while the gradient of the continental rise is typically about 1 in 100.)

Activities While you watch, try to note down (1) the various different uses to which bioluminescence may be put (sequence 5, in particular), (2) the general swimming styles of the various fish (all sequences), and (3) the types of animals shown living on and just above the sea-bed of the continental slope and abyssal plain (sequence 7 onwards). Any notes you make should help you answer questions later on in the text.

Sequence 4 Do you notice anything in particular about the shapes of many of the fish shown here and later in the programme (not including the angler fish)? A possible reason for this characteristic will be discussed in the next section.

Sequence 5 You may have been surprised to see zooplankton so far below the photic zone, but remember that not all zooplankton are herbivores: many live by consuming organic particles or (as demonstrated in this sequence) other zooplankton. The red animal revealed by the red-light 'sniper-scope' is a mysid shrimp (a euphausiid). You may recall from Chapter 3 that the mysid shrimp, and the shrimp and copepods shown shortly afterwards, are all crustaceans, as is the spherical ostracod *Gigantocypris*.

Sequence 6 The 'tiny grazer' shown here is a member of the meroplankton (Section 4.4).

Sequence 7

- As the camera moves down into deeper water, you can see an upright black sponge, and 'plate' corals, whose shape allows them to collect as much light as possible (this is at a depth of 30–40 m). Then there is a large orange sponge and some gorgonians (soft corals) with their polyps withdrawn. The thin yellow 'pipe-cleaners' are probably a type of sponge. Then, hanging down below the small ledge are some grey tube sponges, along with some orange 'blob'-like sponges. At the start of the second 'pan' down the reef, the white feathery animal near the top is a gorgonian.

  In contrast to the brightly coloured sponges shown here, deep-sea sponges are typically brown or grey. Most are 'glass sponges', with highly porous bodies supported by a framework of silica spicules (e.g. *Holtenia carpentaria*, Figure 10.5a); they often have a vase-like shape, tapering to a narrow stalk. Shallow-water sponges have frameworks of calcium carbonate, or of a tough material known as spongin; they often encrust and spread over rocky surfaces, sometimes looking rather like corals.
- We will be discussing the significance of marine snow for deep-sea life in Section 10.3.
- At the top of the continental slope, we see rocks and relatively coarse sediment (sand and pebbles) derived from the land. Lower down, on the continental rise, there are rocks which may have been carried down from the continental shelf in turbidity currents (perhaps as a result of earthquakes) and slabs of layered sediment that may well have slipped from further up the slope/rise.
- The tracks on the sea-bed show where the echinoderms have consumed the marine snow (cf. Figure 10.6). Note the 'tubefeet' of the marching echinoderms.
- The corals shown here are the cold-water corals mentioned in Chapter 7 (to be discussed in Section 10.3). The white coral is the colonial coral *Lophelia pertusa*, which forms large 'reefs'; *Lophelia* is a suspension-feeder. The 'mushroom coral' (so-called because it resembles a mushroom when the polyps are pulled in) is a solitary soft coral, *Anthomastus ritteri*. It preys on zooplankton.
- As mentioned in Chapter 1, surprising as it may seem, tunicates belong to the same phylum as humans – the Chordata. The narration suggests that this tunicate is unique in being predatory but, to survive in an environment where the supply of organic particles is limited, several groups of animals which are filter-feeders in shallow waters have deep-sea representatives that are predatory. These include various tunicates, sponges that entangle their prey, and bivalves that capture their prey using sticky tentacles.
- The narration refers to polychaete worms normally being 'stuck firmly in the sediment'; this is a reference to the fan-worm type of polychaete (which live in tubes in sea-bed sediment, as well as in various other places).
- The 'sensory pits' on the chin of the chimaera are electroreceptors (Section 6.5).
- Note how the clouds of sediment sent up by the six-gilled shark are much finer grained than the sediment of the continental shelf and upper slope

shown earlier. (Some of the close-up shots of echinoderms etc., where the sediment looks rather coarse, may well have been filmed in a pressurised aquarium.)

- There are about 20 species of hagfish, some of which live in burrows. The mouth of a hagfish is armed with a retractable cartilaginous plate which bears two pairs of comb-shaped horny teeth which are used to grasp food and convey it into the mouth. Although hagfish are usually thought of as simply scavengers, much of their diet consists of worms and other invertebrates.

Sequence 8

- In the close shots of the hagfish near the beginning, you can clearly see their sucker-like mouths, around which are four pairs of short sensitive tentacles. You can also see the large slime glands along their flanks – hagfish produce a great deal of slime. (You may recall from Section 6.1 that, despite their cartilaginous skeletons, hagfish are not related to sharks and rays but belong to the Agnatha.)
- For reasons which should become clear, we will be deferring discussion of the community living on the whale skeleton until Section 10.4 ('An alternative way of life').

Sequence 10

- The Marianas (or Mariana) Trench is in the western Pacific. It marks the position of a subduction zone (Figure 2.5), and lies seaward of an arc of small islands (cf. left-hand side of Figure 2.6). Ocean trenches are large-scale features, perhaps 100 km across, and their sides slope down relatively gently; what you see here are small-scale fractures in ocean-floor rocks, not views of the trench as a whole.
- Have a close look at the deep-sea octopus.

Question 10.2 To what phylum of animals do the 'sea-lilies' seen in sequence 7 belong? ◀

Question 10.3 Is 'Dumbo' a 'sea-bat' (as described in Section 7.3.2) or the more common type of octopus? How can you tell? ◀

10.2 Another look at buoyancy, fish muscle, sensing and bioluminescence

We will consider deep-sea fish again in Chapter 11, in the context of fishing, so at this point we will simply revisit four topics introduced earlier (Chapters 2, 4 and 6), this time in the context of life in the deep ocean.

Buoyancy

As you saw in part II of 'The Deep', some deep-sea fish manage to conserve energy *and* catch their prey by hanging motionless in the darkness waiting for a meal! To maintain their position in the water column, they need to be neutrally buoyant, with an average density similar to that of seawater – they cannot use dynamic lift if they are motionless (Section 6.3). Angler fish manage to be neutrally buoyant without the aid of a gas-filled swimbladder because they have light bones, and store oils and fats.

Having most components of their bodies greatly reduced in weight is characteristic of many deep-sea fish – often, the only part of the skeleton that is well calcified is the jaws. The muscles of deep-sea fish often have a high water content, and their bodies contain large pockets of a watery fluid which is less dense than seawater – the angler fish and the gulper eel shown in 'The Deep' are both about 95% water. By contrast, hatchetfish and lanternfish, which live higher up in the water column (i.e. above 1000 m, in the twilight zone), both have swimbladders and so can afford to have heavier bodies: they are much less watery and their skeletons are fully calcified.

Do you recall how the swimbladders of many mid-water and deep-sea fish differ from those of most fish living nearer the sea-surface?

The swimbladders of many mid-water and deep-sea fish contain lipids rather than gas (Section 6.3).

Fish muscle

As indicated at the start of Section 6.2, red muscle (used for sustained swimming) is characteristic of fish living in the well-lit surface layers of the ocean; most fish species living below about 500 m have *no* red muscle.

By considering the lifestyle of angler fish, can you suggest why such fish do not need any red muscle?

Fish with the lifestyle of angler fish do not need to swim fast for sustained periods because: (1) they do not hunt down prey (instead, they wait for the prey to come to them); and (2) as they live below the photic zone, they do not need to escape from fast-swimming predators which hunt by sight (e.g. tuna).

In fact, free-living *male* angler fish do have red muscle, because they need to chase down a female!

Sensing and sound

Earlier, we stressed how noisy the oceans are – but is this true of the whole ocean?

Question 10.4

(a) Give *two* completely different reasons why the deep ocean (below 1000 m) is generally much quieter than surface and near-surface waters.

(b) Why are the oceans particularly noisy around 1000 m depth? ◀

Because the deep oceans are relatively quiet, some animals go to great lengths not to draw attention to themselves by disturbing the water (Section 2.1.1). An angler fish waiting for prey is so still that only the tiny movements of its respiratory organs make any sound; by remaining so still, it prevents any noises it produces itself from masking sounds made by approaching prey, and so does not give itself away to the prey. The numerous long 'bristles' which sprout from angler fish (e.g. 'The Deep', sequence 4) carry neuromasts with hair cells which detect water movement (Section 6.5). It is thought that by having arrays of 'bristles' sticking out at various orientations, an angler fish is better able to detect where the prey is in relation to itself.

Not all ways of swimming are equally 'noisy'.

Can you suggest a way of swimming, demonstrated by a number of fish in 'The Deep', which causes relatively little disturbance?

- Swimming in an eel-like fashion, by undulations of the whole body (Figure 6.1), or by undulations of an elongate dorsal and/or anal fin (like those of the knifefish and the bowfin in Figure 6.7). This way of swimming is likely to be 'quieter' than a beating tail, and does not give rise to a train of vortices (Figure 6.2) (or stimulate bioluminescence in smaller organisms that have been disturbed), which other fish (prey or predator) may detect. (Hagfish and rat-tails both swim in this way; you will see other examples in part III of 'The Deep'.)

Being long may also have another advantage in the world of sound, in that a fish with a long body may have a long lateral line (see Section 6.5). There can be more variation in the 'sound signal' received along a long lateral line than along a short one, and long fish may therefore have a greater sensitivity to variations in the wavelength of sound, particularly at longer wavelengths/lower frequencies. This may be one reason for the long bodies of many deep-sea fish, and the strange shape of the gulper eel, with its 'highly sensitive metre-long tail' ('The Deep', sequence 4).

Many deep-sea fish (e.g. rat-tails) have greatly enlarged head canals which form huge sinuses, tuned to lower frequencies. This may be an adaptation for detecting sounds travelling through the sea-bed.

- Thinking back to Section 6.3, can you suggest another way in which deep-sea fish may detect sound?

- In deep water, low-frequency sound may be detected using swimbladders.

As you may recall, certain fish can also use their swimbladders to *produce* sound. Interestingly, for those groups of deep-sea fish that produce sound using their swimbladders (e.g. rat-tails), it is only the species that live just above the continental slope that do this; their relatives living higher in the water column, or over the sea-bed of the abyssal plains, do not. In the case of the abyssal relatives, it could be that the great pressure at these depths means their swimbladders are less elastic, and their membranes are very tightly stretched; consequently, they vibrate at such a high frequency that they produce the deep-sea equivalent of a squeak!

Bioluminescence

In Chapter 4, and part I of 'The Deep', we looked at how animals in the 'twilight zone' of the ocean (specifically the hatchetfish) use bioluminescence to protect themselves from predators. In part II of 'The Deep', you saw more spectacular examples of bioluminescence in the oceans. There are various types of light organs (i.e. photophores) and some animals have three or four different types at different sites on or in their bodies. For example, the firefly squid which appears in 'The Deep' has hundreds of one type of light organ covering its body (probably to provide 'countershading' when viewed from below, like the hatchetfish), and another type of light organ at the end of its tentacles (perhaps for attracting mates or dazzling predators). The optical structures associated with light organs are as complex as those found in eyes, and include lenses and filters, as well as light guides and light pipes (i.e. biological optical fibres) to allow the light to be emitted some distance from the light organ.

How did bioluminescence evolve in the ocean? This is a question which has perplexed scientists for a long time – indeed, Charles Darwin singled it out as something that his theory of natural selection could not account for. Only a few terrestrial organisms produce bioluminescence (these include fireflies and glow-worms, plus some bacteria and fungi), but in the sea it is extremely widespread,

being found at all depths and in a wide variety of organisms, including bacteria and dinoflagellates, jellyfish and comb jellies, sea-pens, squid and fish. In total, organisms from 16 different phyla have been found to produce bioluminescence.

What might this suggest about the evolution of bioluminescence? Is it more likely to have evolved at one point in time and then been carried forward in different groups of organisms, or to have evolved separately in different groups?

It is more likely to have evolved separately in different groups. It is hard to see how a feature found in (say) bacteria, dinoflagellates and squid could *not* have evolved independently in each case.

Bioluminescence is produced as a result of molecules of substances known as luciferins reacting with oxygen, and effectively 'burning up' (there are many types of luciferin – the word just means 'light-bearer'). This reaction would not produce light energy were it not for the presence of an enzyme (a biological catalyst) called *luciferase* (of which there are various types). The luciferase slows down the reaction and allows some of the energy to be released as light, rather than heat. In addition, it coordinates the reactions in the different molecules of luciferin so that they all 'fire off' at once, producing one bright flash instead of lots of small ones.

Most organisms make their own luciferin, while others acquire it in their diet, as we acquire many vitamins. Yet others – including some squid, tunicates and fish – play host to (i.e. have symbiotic relationships with) colonies of luminescent bacteria. However, the key to producing 'useful' light is luciferase, and many marine biologists believe that before bioluminescence evolved, enzymes of this type could already have been present in cells, but performing another function. As luciferase reacts with oxygen, it is possible that it developed from enzymes known as oxygenases, and was originally involved in making oxygen available for respiration, or perhaps in metabolising toxic substances.

A more recent theory about the evolution of bioluminescence concentrates on the luciferin. The most abundant type of luciferin is a very simple one which was first isolated from a jellyfish (*Aequoria victoria*). Because jellyfish are sometimes classified as coelenterates, this luciferin is called coelenterazine. Coelenterazine is also found in comb jellies, sea-pens, and some fish and squid, all of which acquire it in their diets – although no-one knows from what. Experiments with coelenterazine have shown that it reacts vigorously with, and destroys, oxygen-carrying molecules known as free radicals, which are themselves highly reactive and can destroy DNA and cell membranes, and generally cause cells to age and die prematurely. The ocean has high concentrations of free radicals because they are produced in surface layers by the action of ultraviolet light on water, and are also a by-product of metabolic processes. The new theory is that coelenterazine initially evolved as a defence against free radicals, a defence particularly needed in near-surface waters. Over time (so the theory goes), animals moved deeper into the ocean, into regions of permanent darkness. Coelenterazine's defence role was no longer so necessary, but there *was* an evolutionary pressure for the development of means of communication. Gradually, over time, and in numerous different organisms, the role of coelenterazine changed to the production of bioluminescence.

Question 10.5 On the basis of parts I and II of 'The Deep' (and Section 4.2.2), make a list (in note form) of the different ways in which twilight-zone and deep-sea animals use bioluminescence. (You should be able to come up with at least three or four uses.) ◀

Other animals' bioluminescence may be a hazard for a deep-sea fish, even if those animals are not actively looking for food. For example, as alluded to above (in the context of 'quiet swimming'), the flashes of animals that have been accidentally disturbed can give away a fish's presence. There is a particular problem for transparent animals, in that bioluminescent prey may carry on bioluminescing *after* it has been swallowed! It is thought that this is why many transparent carnivores have red pigmentation, strategically positioned to hide the giveaway flashing of animals inside them.

10.3 Is there spring in the deep sea?

Until well into the 20th century, the deep sea was assumed to be a constant, unvarying environment: it was thought that the sea-bed was never disturbed by strong currents; that deep-sea temperatures never varied (at least not on short time-scales); and that the rain of fine sediment (clay and organic matter) falling from above arrived at a more or less constant rate, both spatially and over time, regardless of what was occurring in surface waters. In summary, the deep ocean was regarded as hostile and unchanging, with deep-sea animals living slow, monotonous lives.

It is now known that the deep sea is by no means unchanging. Strong frontal currents like the Gulf Stream, and the eddies that spin off them (Section 5.4.1), extend to depths of several thousand metres: the sediment on the continental slope and rise is known to be disturbed by such eddies, producing so-called 'abyssal storms'. Deep-sea sediments are often shaped into ripples, indicating the flow of water over the sea-bed: this could be a tidal current (remember that the forces that give rise to the tides are felt throughout the body of the ocean; Section 3.1) or the flow of cold dense water (e.g. AABW) spreading away from high latitudes. The most dramatic events to occur at the sea-bed are probably the arrival of enormous amounts of sediment (clay, silt, sand and boulders) carried down from the edge of the continental shelf in turbidity currents. As mentioned in Section 2.3, the continental rise and the abyssal plains are built up of great thicknesses of sediment deposited by turbidity currents over millions of years.

But what of the food supply in the deep ocean – is that unvarying? Before moving on to address that question, consider for a moment what types of animals live on and above the deep sea-bed, and the feeding strategies that animals in the deep sea must use.

Question 10.6

(a) (i) Thinking back to part II of 'The Deep', what types of animals did you observe living on and above the deep sea-bed of the continental slope/rise and abyssal plain (i.e. after the track down over the edge of the reef (sequence 7 onwards))? You may have noted these down. (You do not need to include the fauna associated with the dead whale, or with the hydrothermal vents and 'brine lake' shown in part III.)

(ii) On the basis of 'The Deep', which invertebrate phylum would you say dominates the deep sea-floor?

(b) What feeding strategies (cf. Section 3.3) did you see being employed by deep-sea animals in part II of 'The Deep', and by which animals? Try to come up with at least four different categories. (You don't need to identify the feeding strategy of every single animal shown.) ◀

So, most animals in the deep sea rely on organic remains that sink down from the photic zone. Much of this organic material is consumed by animals in the water column, and decomposed by bacteria. Only a small percentage of what sinks from the surface survives to reach the deep sea-floor, where it is consumed by deposit-feeders and suspension-feeders, and decomposed by bacteria living in the sediment (which are also themselves consumed).

As shown in 'The Deep', suspension-feeding sea-lilies are typically found attached to rocky areas on the continental slope, in places where currents are relatively strong (sequence 7).

Thinking about their food supply, can you suggest why these animals favour areas of sea-bed where the current is relatively strong? *Hint* Consider whether they are likely to be passive or active feeders (cf. Section 3.3).

As food is relatively scarce, suspension-feeders in the deep sea cannot afford to spend energy on catching food: they are passive feeders. They therefore need to live where currents will bring them a reliable supply of food. (In addition, currents can sweep away any sediment that might clog up their filtering apparatus.)

'Reef-building' cold-water corals are also suspension-feeders. The narration in 'The Deep' suggests that they are a new discovery, but cold-water corals have been known about for a long time. Wyville Thomson included an illustration of *Lophelia pertusa* in *The Depths of the Sea*, and broken cold-water corals have been brought up in trawl nets for some time. However, it has only recently become clear how widespread and abundant they are. Large 'reefs' have been found in various locations around the world, particularly along the continental slope (including that off the western/north-western British Isles); because of their locations, they are often found by oil companies. The largest reef so far (occupying an area of about 100 km^2) was found in 2002 off Røst Island in the Lofoten archipelago, off north-western Norway. The best developed reef in European waters is the Sula Reef, off western Norway – this is 13 km long and in places rises 30 m above the sea-bed. (The locations of the Røst Reef and Sula Reef are shown in Figure 11.27.)

All the animals discussed in the answer to Question 10.6 may be described as megafauna – relatively large animals that can be seen with the naked eye.

Bearing in mind that they were filmed moving *over* the sea-bed, what other term could you use to describe sea-urchins, sea-cucumbers, etc. (Section 2.3)?

These animals may be described as *epifauna*.

The most numerous animals in the deep sea are actually the infauna, rarely captured on camera. Large numbers of crustaceans and worms (including nematodes and polychaetes), ranging from megafauna to microscopic animals, live within the sediment. The sediment-living fauna is extremely diverse, and it seems that new species are continually being discovered. We will not say any more about these animals here.

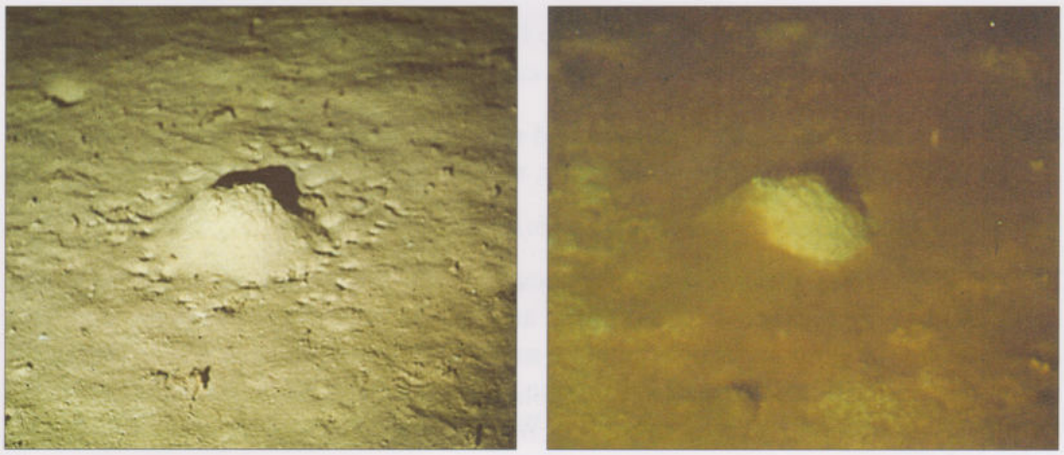
Now let's return to the theme of the supply of food to the deep ocean. The bulk of organic material that sinks to the deep sea-bed consists of dead and dying phytoplankton and zooplankton, along with faecal pellets of zooplankton and larger animals. These are mostly so small that they would take months or even years to sink to the sea-bed, and would be carried laterally by ocean currents as they fell, so

there would be no correspondence between the area of sea-surface where the remains originated and where they eventually ended up. For this reason, it was long assumed that deep-sea organisms received a continual fine 'rain' of particles, and would be completely isolated from what was happening in surface waters.

In the early 1980s, an innovative deep-sea time-lapse camera system, known as 'Bathysnap', was deployed in the Porcupine Seabight, a marked depression in the continental rise to the south-west of Ireland, attaining depths of ~ 4000 m. (The Porcupine Seabight is the cause of the indentation of the 2000 m contour in the bottom left-hand corner of Figure 3.4; it opens out onto the Porcupine Abyssal Plain.) The results from Bathysnap were very exciting; although many of the animals photographed had been seen before, they had never been observed in their natural habitat. Even infaunal animals (none of which appear in 'The Deep') were recorded making occasional forays out onto the sediment surface; others were detected through the efforts of predatory animals to dig them up.

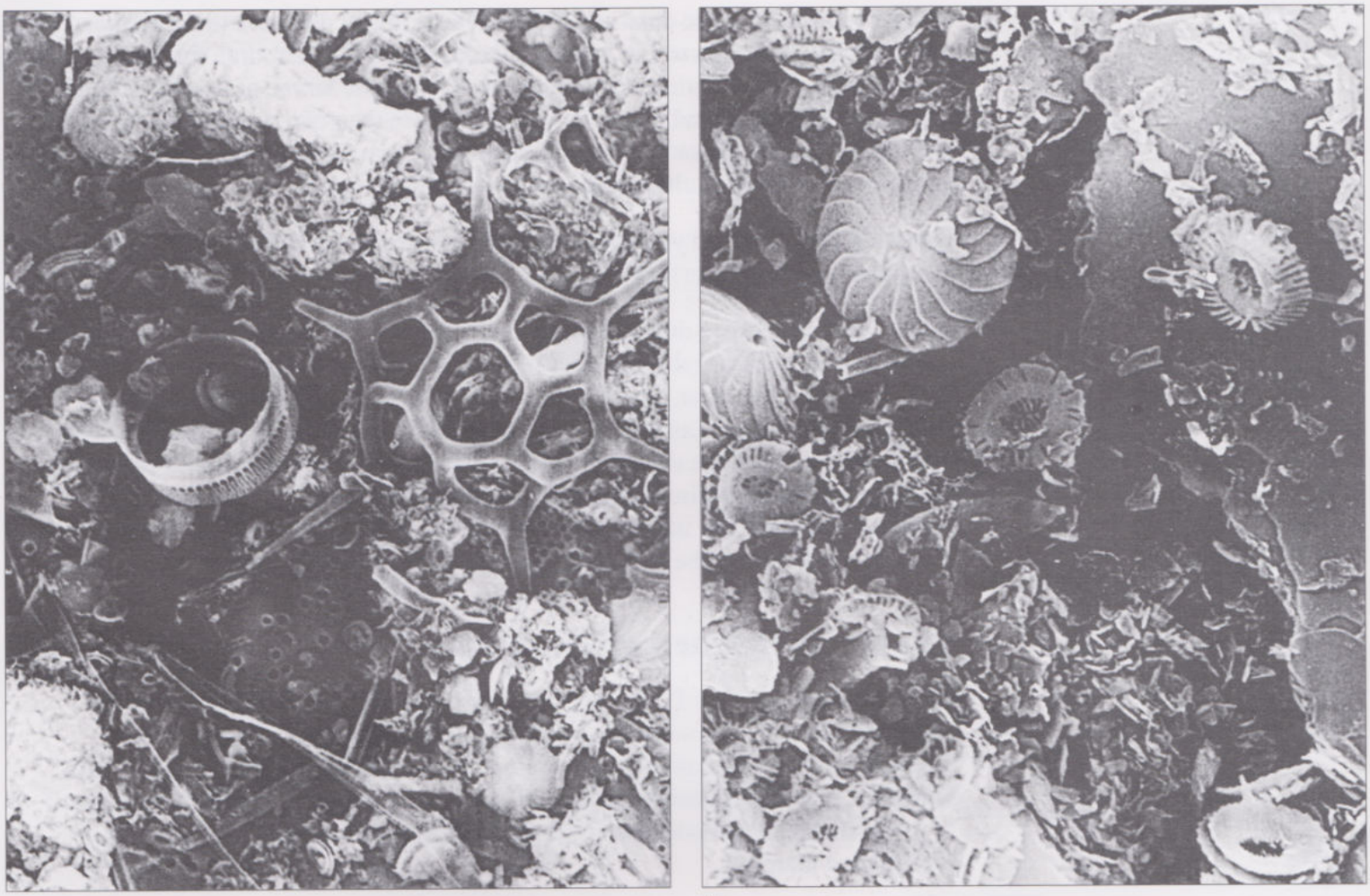
The photographs also recorded that certain animals were active at particular times during the tidal cycle, apparently because they were responding to changes in tidal currents. This was particularly interesting because it indicated that animals might also respond to changes in bottom currents, especially as such changes could bring water slightly warmer or cooler than usual (though still about 2 °C). However, as far as supplies of food to the deep sea-floor were concerned, no variability was detected at all – but in any case, it was not expected.

As it happened, for several years the research cruises to the Porcupine Seabight and Porcupine Abyssal Plain had taken place between October and April. Then in 1981, 1982 and 1983, the cruises took place in May and July, and the situation observed was quite different. The time-lapse Bathysnap pictures showed that the sea-floor would suddenly become covered with a dark, greenish, fluffy material (Figure 10.6), which after a few weeks began to disappear again, as it was consumed by sea-bed animals. The suspicion that the green fluff was debris from the spring plankton bloom was confirmed when, having been collected by a specially designed sediment-corer, it was examined under the microscope (Figure 10.7).



(a) (b)

Figure 10.6 Bathysnap time-lapse photographs taken in spring 1983 (15 June and 14 July), at 4000 m depth in the Porcupine Abyssal Plain. May and June, greenish fluffy material began to accumulate in hollows and around mounds (the mound shown, made by an animal, is about 10 cm across). By mid-July, the sea-bed was completely covered by a carpet of fluff. By mid-August, the fluff had begun to disappear again. (At the bottom of (a), you can just see the tracks of various worms.)



(a) (b)

Figure 10.7 Photographs taken under the microscope of the debris from the spring bloom, collected from the sea-bed at a depth of 1450 m in the Porcupine Seabight in late June 1985. (a) The topmost layer of fluff (magnification × 650). Amongst the unidentifiable amorphous material, you can see the siliceous remains of diatoms (the 'ring' and the 'snowflake' to the right of it). (b) Older detritus from the next layer down (magnification × 2400), which contains a higher proportion of unidentifiable amorphous material, and fewer siliceous remains.

Thinking back to Chapter 1, can you suggest what the disc-like objects (some with holes in the middle) in Figure 10.7b might be?

They are the calcium carbonate plates, or coccoliths, from various species of coccolithophore (cf. Figure 1.9). (There are also some coccoliths in Figure 10.7a, but as this is at a lower magnification, they are hard to see.)

Well done if you guessed this!

So, there was no doubt that the fluff was phytoplankton debris, and given the timing of the spring bloom, it must have sunk from surface waters in a matter of weeks, at speeds of greater than 100 m day^{-1} – at least ten times faster than had been thought possible, given the small sizes of the remains (e.g. coccolithophores are ~5 microns across; Figure 1.9). We now know that the debris from plankton blooms aggregates into masses which sink much faster than would be possible for individual cells. These fluffy aggregates are the 'marine snow' mentioned in Section 4.3, which can be clearly seen during some of the Blue Planet programmes, including 'The Deep' and 'Seasonal Seas'. Figure 10.8 shows a typical 'snowflake', collected in the Atlantic.

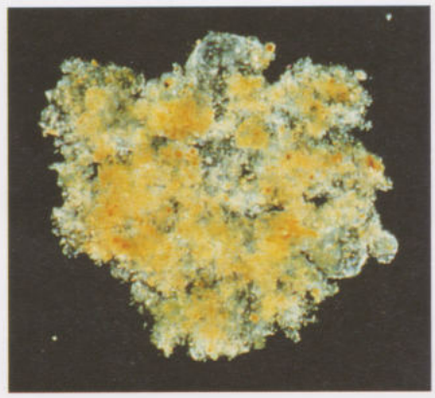


Figure 10.8 An aggregate of marine snow, photographed in the laboratory. It is made up of dead and decaying phytoplankton, zooplankton faecal matter and zooplankton shells, and bacteria; it is ~ 4 mm across.

So, there is spring in the deep sea. What is more, many deep-sea invertebrates produce planktonic larvae (i.e. meroplankton, Figure 4.12) in time for them to take advantage of the springtime food bonanza. (Planktonic larvae of benthic animals that spawn all year round generally spend no more than two weeks in the plankton, and rely on large yolk-sacs to sustain them until they settle on the sea-bed. Some young are miniature adults and do not have a larval stage.)

Question 10.7 Would you expect there to be springtime falls of marine snow everywhere in the ocean? ◀

It may have struck you that marine snow provides a strong link between physical conditions and biological productivity in surface waters on the one hand, and life in the deep sea on the other, and that, far from being isolated from environmental changes at the surface (as Wyville Thomson believed), animals in the deep ocean feel at least some of the effects of surface events almost immediately. Furthermore, as the pattern of deep circulation (Figure 10.4) is driven by conditions at the surface, even the water masses flowing over the deep sea-bed are determined by climatic conditions at the surface where the water originally sank (Section 10.1).

10.4 An alternative way of life

In the final part of 'The Deep', you will see some deep-sea ecosystems whose existence was not even suspected until the 1970s, and which are only now beginning to be systematically explored on any scale. Before watching this final sequence, you will probably find it useful to look at Figure 2.5 to remind yourself of the positions of the mid-ocean ridges (constructive margins) and trenches (destructive margins).

▶▶ If you have not already done so, you should now look at the final part of 'The Deep' on DVD 1. As with part II, we recommend that you begin by reading the 'General note' and then watch all of part III. Then read through the notes relating to the various sequences, and play those sequences (or parts of them) again if you wish. ◀◀

Notes on the 'The Deep' (part III)

General note This part of 'The Deep' begins with an animation showing a submersible descending into a steep-sided valley, representing the rift valleys that extend along much of the axis of the spreading-ridge system. In reality, the sides of axial rift valleys slope much more gently than shown here, and the valleys are generally wider: the rift valley along the axis of the Mid-Atlantic Ridge is 25–30 km across and 1–2 km deep; the one along the axis of the East Pacific Rise is less than 1 km wide and less than 100 °m deep (and is sometimes absent altogether). If you are not convinced that this is animation, think about the scale of the Mid-Atlantic Ridge, and about how far light travels through water!

Sequence 11

- The 'once molten rock' shown near the start of this sequence is in the form of 'pillow lavas'. As will be discussed in the text, the appearance of these particular pillow lavas is somewhat atypical.

- The 'towering chimneys pouring out water as hot as molten lead' are known as 'black smokers'. Black-smoker chimneys are generally much smaller than these appear to be – some are only 1–2 m high.
- The 10 cm-long 'Pompeii worm' (which has been given the name *Alvinella pompejana*) is the most heat-tolerant animal so far discovered. It burrows into the sides of smoker chimneys, and produces the white papery tubes to live in. Water from inside the vent flushes through the tubes, with the result that the worm's tail may be at temperatures of ~80 °C, while its head at the tube entrance may be at ~14 °C. It seems that it is able to withstand the high temperatures with the help of a 'fleece' of bacteria which covers its back, producing some degree of insulation. The bacteria are sustained by mucus produced by tiny glands on the worm's back.
- The spectacular red and white tubeworms (*Riftia pachyptila*) will be discussed in the next section. The small particles rising upwards around the tubeworms (and also seen in other shots) are bits of organic debris (fragments of bacterial mats etc.) being carried up in the warmed water, which is rising because it is less dense than the surrounding water (cf. Figures 10.11 and 10.13).
- Surprisingly few fish have been found in association with hydrothermal vents, and those that have been spotted have proved difficult to catch. The pale pink fish seen peeping out from the clump of tubeworms, and swimming in and out, is a type of 'eelpout' (eelpouts are found in various other marine and freshwater environments).
- As far as mid-ocean ridges are concerned, 'The Deep' focuses on the fauna at hydrothermal vents, because very little is known about other animals living along ridge axes, either on the rocky sea-bed or in the overlying waters. Efforts are being made to remedy this through an extended international research project, known as MAR-ECO, which is investigating the distribution and ecology of animals and animal communities (including fish, crustaceans, zooplankton and gelatinous animals) along the Mid-Atlantic Ridge between Iceland and the Azores; it is also studying how animals behave in relation to currents and the topography of the ridge (e.g. one project is investigating the extent to which whales use the Mid-Atlantic Ridge as a migration corridor).

Sequence 12 You might be interested to know that the brine lake was formed from water originally trapped in sediments, and forced by pressure to migrate through a layer of evaporites – salt layers deposited about 200 million years ago, early in the opening of the Atlantic when the Gulf of Mexico was a very shallow sea. The high biological productivity associated with the lake is the result of a 'cold seep' at the same site (i.e. the lake itself is not the cold seep). Cold seeps, and the source of the methane, will be discussed in Section 10.4.2.

10.4.1 The search for hydrothermal vents brings surprises

By the early 1970s, the theories of plate tectonics and sea-floor spreading (Figures 2.5 and 2.6) had been accepted by most Earth scientists, but it was not known just how new sea-floor is formed at spreading ridges. In 1974, a joint French–American expedition was launched to examine the sea-bed close up, and map it rather as would be done in geology on land. In a ground-breaking expedition, given the acronym FAMOUS (French–American Mid-Ocean Undersea-Study), the bathyscaph *Archimède*, the deep-diving submarine *Cyana,* and the submersible *Alvin* (Figure

10.1), operated by Woods Hole Oceanographic Institution, descended to the crest of the Mid-Atlantic Ridge some 640 km south-west of the Azores (cf. Figure 2.5).

Entering the rift valley that extends along the crest of the ridge, the scientists were amazed at what they saw through their vessels' tiny portholes. It was like 'driving in first gear through a light snowfall at night', but the scenery was dramatic and unexpected. One wall of the rift valley loomed up out of the darkness, while the valley floor was criss-crossed with crevasses and faults running between volcanic hills – indications that the sea-floor was being pulled apart. The flanks of the volcanoes were made up of basaltic pillow lavas, the lava formations mentioned in the Notes on part III of 'The Deep'; basalt is the rock-type produced by sea-floor volcanism. Pillow lavas have characteristic bulbous shapes (Figure 10.9) because when hot basalt is extruded at the sea-bed (rather like toothpaste squeezed from a tube) its outer surface is chilled by the cold water, and solidifies extremely fast. The inside of the 'pillow' is protected from the cold water and crystallises much more slowly. However, in the case of the pillow lavas shown in 'The Deep', the outer 'shells' seem to have collapsed or broken, allowing the molten lava inside the pillows to flow out before solidifying.

Figure 10.9 Some typical pillow lavas.

Given the widespread evidence of volcanic activity, the expedition's oceanographers expected that somewhere in the rift valley they would find unusually warm water emerging from the sea-floor. It was presumed that seawater seeping down through cracks and fissures would become heated by the source of the lava that was erupting at the sea-bed to produce the pillow lavas. On being heated, the percolating water would become less dense and rise back up through cracks and fissures (that is, it would convect), and escape at the sea-floor. Such hydrothermal activity (but involving heated groundwater) is found in volcanic areas on land; some of its most spectacular manifestations are the hot springs and geysers of Iceland, which straddles the Mid-Atlantic Ridge (cf. Figure 2.5). In fact, no hydrothermal activity was observed on this expedition, although there was indirect evidence in the form of basalt that seemed to have been chemically altered by contact with hot seawater.

This pioneering expedition proved the value of going down to see the deep-sea environment at first hand, and over the next few years *Alvin* was used in a number of expeditions to investigate the Galápagos spreading axis, between the Cocos Plate and the Nazca Plate, in the Pacific Ocean (Figure 2.5).

- Can you suggest why, having failed to find hydrothermal activity at the Mid-Atlantic Ridge, the *Alvin* scientists thought that they might have more success at the Galápagos spreading axis? *Hint* The lengths of the arrows in Figure 2.5 are proportional to the speed of plate movement.

- The arrows corresponding to movement of sea-floor away from ridges in the Pacific are significantly longer than the arrows corresponding to movement away from the Mid-Atlantic Ridge. This suggests that at Pacific ridges (e.g. the East Pacific Rise and the Galápagos spreading axis), hot magma is being supplied to form new ocean floor at a greater rate than at the Mid-Atlantic Ridge. With a greater supply of heat to the ridge crest, evidence of hydrothermal circulation is likely to be easier to find.

You might be interested to know that in the Pacific, sea-floor is spreading away from the East Pacific Rise at a rate of about 6–8 cm y^{-1}, as compared to 1–2 cm y^{-1} for the Mid-Atlantic Ridge; you can check these speeds by comparing the lengths of the relevant arrows in Figure 2.5 with the length of the one in the key (which represents a speed of 5 cm y^{-1}).

At the Galápagos spreading axis, *Alvin*'s first dive was to a site known as the 'Clambake' because sea-bed photographs showed that it had more than average numbers of clamshells, thought perhaps to be the remains of a clambake on a passing ship. At the Clambake, *Alvin*'s heat sensor detected a tiny increase in temperature, just a fraction of a degree Celsius. Immediately afterwards the scientists realised that – to their amazement – they were surrounded by a great abundance of strange animals. Along with the clams (now seen to be enormous) were creatures unlike anything ever seen before, including pale orange animals resembling dandelions gone to seed, and white crabs and lobsters. At a nearby site, later named 'The Garden of Eden', they found more strange animals, of which the most striking were red tubeworms, like those shown in 'The Deep' (sequence 11). These were certainly hydrothermal vents, although the waters in which the strange animals were living were only slightly warmer than the 2 °C of the surrounding water.

Everyone was mystified as to what could be supporting such prolific life, so far from the sunlit surface layers. One theory was that the 'updraft' of warm water from the vents drew in such large volumes of water from above the surrounding sea-bed that the area had more than its share of organic material from the surface (you can see particles being carried by such an updraft in 'The Deep'). This idea was dismissed because there were so many large animals around the vents that the community could not possibly be supported in this way.

A clue was provided when a sampling bottle containing water collected from near the vent was opened back at the surface, and the ship was filled with the repulsive 'rotten eggs' smell of hydrogen sulfide. The tubeworms were found to have large numbers of sulfide-oxidising bacteria in the equivalent of their guts, and their red 'plumes' turned out to be like gills, but capable of extracting not only oxygen from seawater, but also hydrogen sulfide; the clams and mussels were also found to have sulfide-oxidising bacteria in their gills; and so on. These bacteria were living in the animals symbiotically, so that both the bacteria and the host animals were benefiting.

It was deduced that the chemical energy released by the oxidation of hydrogen sulfide (and of other sulfides and methane, also emerging from the vents) was being used by the bacteria to build organic molecules such as carbohydrates. Using chemical energy to build organic material is known as *chemosynthesis*.

The 'word equation' for this type of chemosynthesis would be:

$$\underset{\text{(from solution in seawater)}}{\text{carbon dioxide}} + \underset{\text{(from vents)}}{\text{hydrogen sulfide}} + \underset{\text{(from solution in seawater)}}{\text{oxygen}} + \text{water} \xrightarrow{\text{chemical energy}} \text{carbohydrates} + \underset{\text{(to solution in seawater)}}{\text{hydrogen ions}} + \text{sulfate ions} \quad (10.1)$$

The vent bacteria are described as 'sulfide-oxidising' because oxidation is defined as *the addition of oxygen and/or the removal of hydrogen*. The bacteria take in hydrogen sulfide (H_2S), remove the hydrogen from it, and combine the remaining sulfur (S) with oxygen from seawater to make sulfate ions (SO_4^{2-}). (The chemical equation which describes this process is given at the top of Figure 10.10b.)

You may have spotted that equation 10.1 has some similarities with the equation for photosynthesis (equations 1.1a, 4.1), as well as some differences:

$$\underset{\text{(from solution in seawater)}}{\text{carbon dioxide}} + \text{water} \xrightarrow{\text{light energy}} \text{carbohydrates} + \text{oxygen} \quad (1.1a)$$

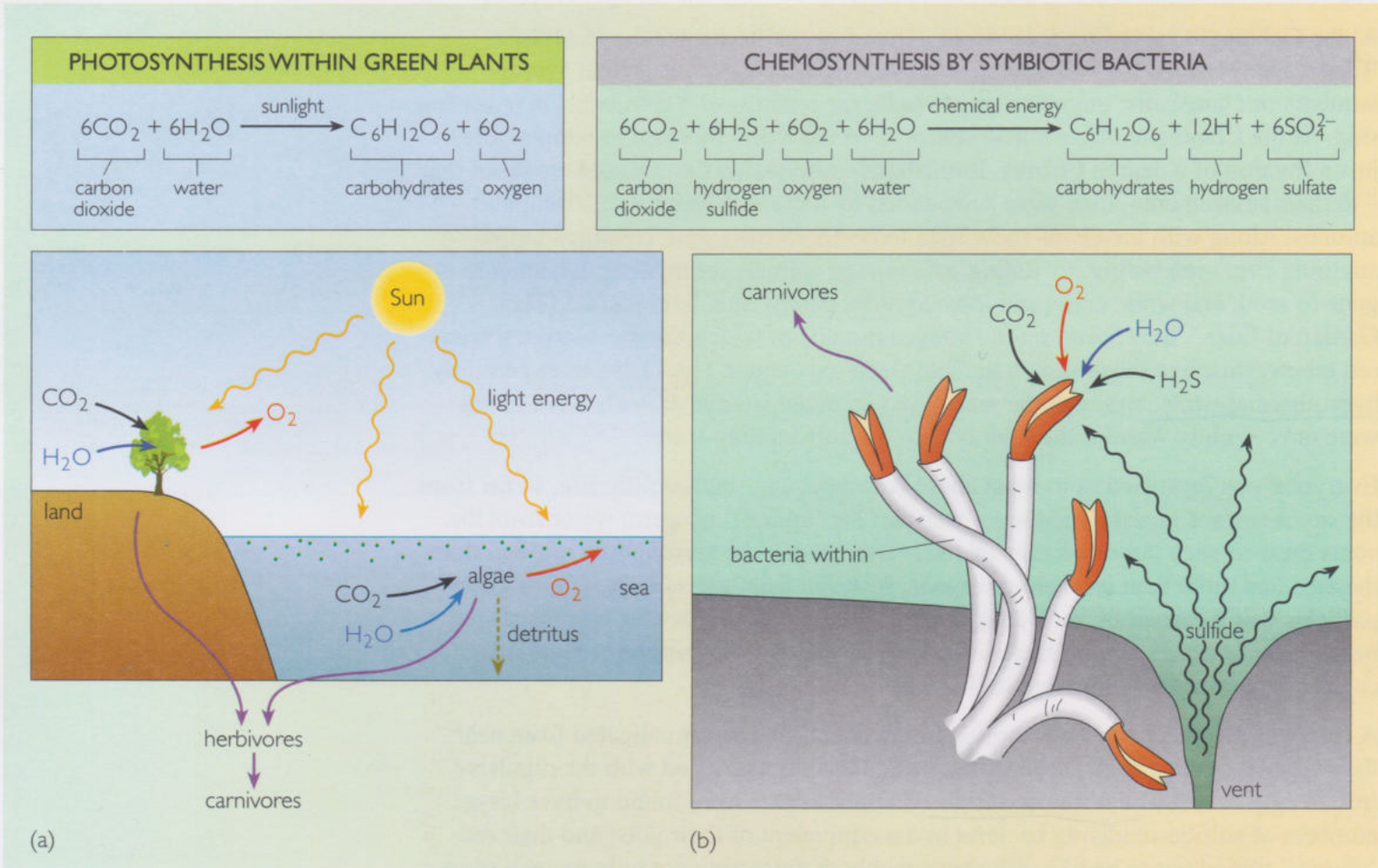


Figure 10.10 Comparison of a hydrothermal vent system (represented here by a group of tubeworms), driven by sulfide-oxidising bacteria, with an ecosystem driven by sunlight. In (a), the energy for the production of carbohydrates comes from the Sun (photosynthesis); in (b), the energy for carbohydrate production comes from sulfide-oxidising bacteria (chemosynthesis).

Figure 10.10 compares a hydrothermal vent ecosystem with a 'conventional' ecosystem supported by photosynthesis on land and in sunlit waters. If you can't follow the chemical equations given at the top, just study the diagrams.

What *similarities* are there between chemosynthesis and photosynthesis?

In both cases, carbon dioxide (CO_2) and water (H_2O) are used to provide the carbon, hydrogen and oxygen (C, H and O) needed to build carbohydrates ($C_6H_{12}O_6$).

The big difference is that production of carbohydrates by chemosynthesis *also* requires hydrogen sulfide (H_2S) plus oxygen (O_2) to oxidise it, so releasing chemical energy to be used in the building of carbohydrates. In the case of photosynthesis, the Sun's energy is used to break up water molecules to release hydrogen, and then combine it with carbon dioxide to make carbohydrates (*liberating* oxygen in the process).

Hydrothermal vents like those discovered at the Clambake and the Garden of Eden are known as warm-water vents, because the fluid emerging at the sea-floor is at a fairly moderate temperature of ~ 10–25 °C. Figure 10.11 shows schematically what is believed to occur in the sea-bed below warm-water vents: hydrothermal fluids originate as ordinary seawater, heating up and exchanging ions with the hot rock as it flows through it, so that its composition (and that of the rock) changes. If the fluid circulates for a sufficiently long time, it eventually reaches chemical equilibrium with the rock, i.e. although ions continue to move from rock to water, and vice versa, additions and removals of ions cancel out, and the compositions of both the rock and the fluid stop changing. At this point, we have very hot 'neat' hydrothermal fluid, at temperatures of perhaps 100–400 °C. However, as the fluid moves towards the sea-bed, it mixes with a much larger volume of cold seawater that has locally percolated down through cracks and fissures; the diluted fluid that emerges from the sea-floor is therefore significantly cooler than the original 'neat' fluid, and has a temperature and composition fairly close to those of ordinary seawater.

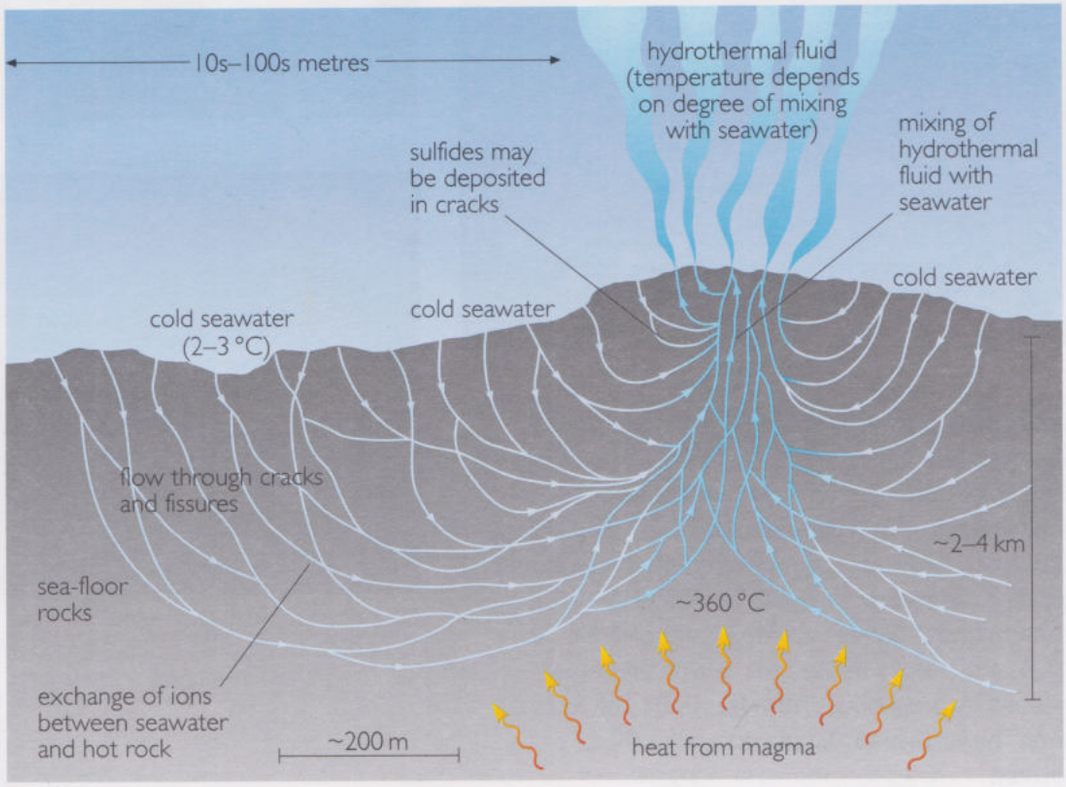
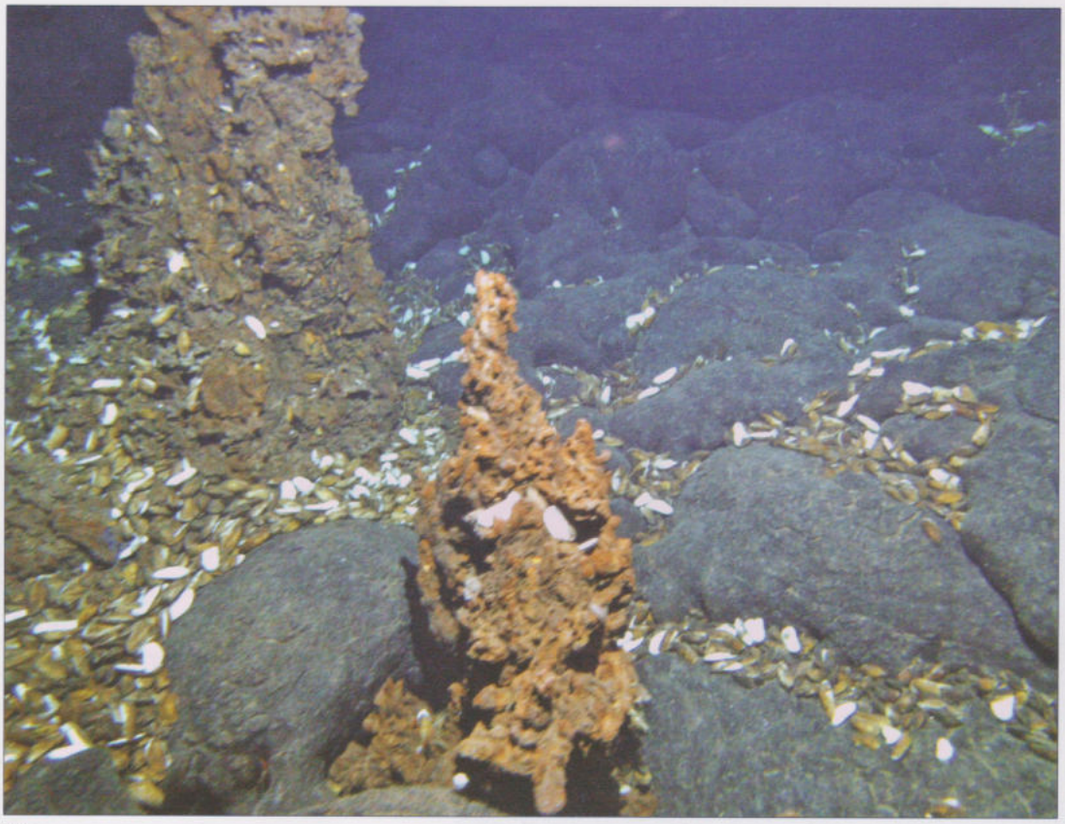

10s–100s metres
hydrothermal fluid (temperature depends on degree of mixing with seawater)
sulfides may be deposited in cracks
mixing of hydrothermal fluid with seawater
cold seawater
cold seawater
cold seawater (2–3 °C)
flow through cracks and fissures
~2–4 km
sea-floor rocks
~360 °C
exchange of ions between seawater and hot rock
~200 m
heat from magma

Figure 10.11 Schematic diagram to illustrate hydrothermal circulation, showing how hot hydrothermal fluid mixes with seawater before emerging at the sea-bed at warm-water vents.

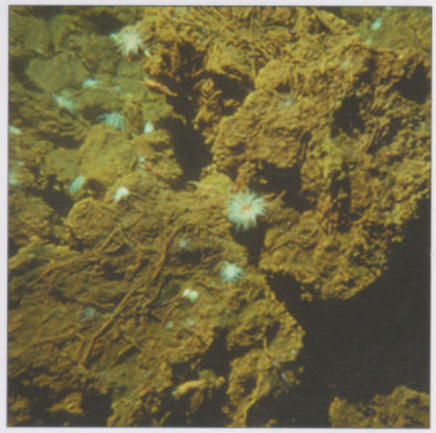
Researchers studying the warm-water vents measured the concentrations of various ions in the fluid emerging at the mouths of the vents. These included sulfate and magnesium ions (SO_4^{2-} and Mg^{2+}), both of which are removed from seawater circulating in the hot rock (they combine with constituents of the rock to form new minerals), and silica (SiO_2), which is added to seawater from the hot rock. These chemical measurements allowed the researchers to estimate the degree of dilution of neat hydrothermal fluid that had occurred within the crust of the Galápagos spreading axis (cf. Figure 10.11), and hence to estimate the temperature of undiluted vent fluid. As a result of their calculations, they predicted that if vent fluid could somehow reach the sea-bed *without* mixing with cold seawater within the ocean crust, it would emerge at a temperature of about 360 °C.

This proved to be the case: later the same year (1979), *Alvin* scientists found vents gushing fluid at a temperature of ~350 °C at 21° N on the East Pacific Rise (Figure 2.5). These vents, to be named 'black smokers', were similar to the one shown in the final part of 'The Deep' (sequence 11); their 'chimneys' were made of colourful sulfides and oxides of iron, manganese, copper and zinc, and the 'smoke' billowing



(a)

(b)



(c)

Figure 10.12 (a) Hydrothermal chimneys, which formed amongst pillow lavas at a depth of about 1670 m on the Galápagos spreading axis at ~90° W. The chimneys are now inactive, and the empty mussel shells lying amongst the 'pillows' suggest that some or all of the associated vent fauna have died or moved to another vent. The orange coating on the chimneys is iron oxide (i.e. rust). (b) Recently active chimneys at a vent field at 26° N on the Mid-Atlantic Ridge. The chimneys are made up of metal sulfides, and have a coating of iron oxide; the white material on the outside of some of the chimneys may be anhydrite (Figure 10.13). (c) Blocks of sulfides of iron and other metals, coated with iron oxide, and colonised by anemones (from the same site as (b)). It was not clear whether the thin worms on the surface of the blocks were still alive. All three photographs were taken from *Alvin*.

out of them was found to consist of particles of sulfides of iron, manganese and other metals, along with oxides and hydroxides. In fact, chimneys of recently extinct black smokers had been found on the Galápagos spreading axis, but at the time it was not clear what these tall pinnacles resembling stalagmites were (they were similar to those shown in Figure 10.12).

Black smokers form because precipitating minerals (i.e. minerals forming from ions coming out of solution into solid form) have blocked up most of the cracks through which seawater could percolate down to mix with the rising hydrothermal fluid (cf. Figure 10.11). Precipitation of these minerals (which include sulfides, anhydrite ($CaSO_4$) and silica (SiO_2)) continues on the sea-floor, so that a chimney builds up around the vent (Figure 10.13). Because the fluid is discharged into the overlying seawater without having had the chance to mix with seawater, it is still close to its original temperature. Being very hot, it is of relatively low density compared with the surrounding water, and is therefore buoyant. As it rushes up into the overlying seawater, there is a great deal of turbulent mixing between the two, and the rising plume draws in seawater from the surrounding area. This is why black smokers are so dramatic, unlike the gently flowing fluids of warm-water vents.

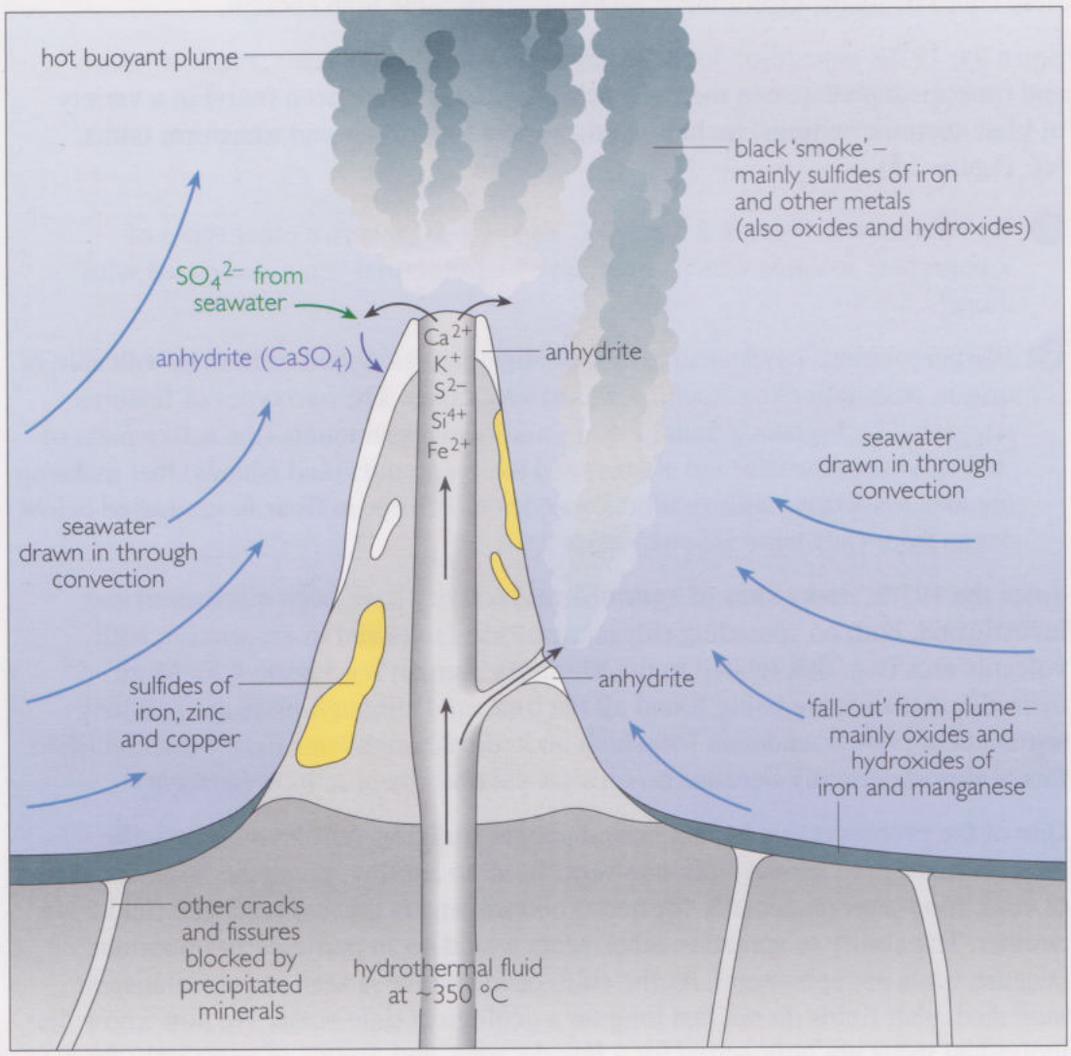

hot buoyant plume
black 'smoke' – mainly sulfides of iron and other metals (also oxides and hydroxides)
SO_4^{2-} from seawater
anhydrite ($CaSO_4$)
Ca^{2+}
K^+
S^{2-}
Si^{4+}
Fe^{2+}
anhydrite
seawater drawn in through convection
seawater drawn in through convection
sulfides of iron, zinc and copper
anhydrite
'fall-out' from plume – mainly oxides and hydroxides of iron and manganese
other cracks and fissures blocked by precipitated minerals
hydrothermal fluid at ~350 °C

Figure 10.13 Schematic cross-section through an active black smoker. The chemical composition of the chimney and the 'smoke' varies from place to place, and depends on the composition of the hydrothermal fluid, which in turn depends on the composition of the rocks through which it flowed, the temperatures at which the rocks and fluid interacted, and other aspects of environmental conditions in the ocean crust in the vicinity of the vent.

The discovery that certain elements are added to seawater at hydrothermal vents, while others are lost to the ocean crust, was of great interest to geochemists. As you know from Section 2.1, most of the dissolved constituents in the ocean are supplied by rivers; however, the ocean contains more of certain elements than can be accounted for by river flow, and less of others. It was now known for sure that (as many geochemists had suspected) these discrepancies could be accounted for by hydrothermal activity.

The precipitation of metallic compounds at hydrothermal vents produces what are in effect ore deposits of valuable metals; indeed, some extensive ore deposits on land are now recognised as being produced as a result of hydrothermal circulation through oceanic crust. At present, the cost of extracting metal ores from the deep sea would be exorbitant, but this could change with the development of the appropriate technology. As indicated in Figure 10.11, hydrothermal activity extends down 2–4 km and affects the sea-bed for as much as 1 km either side of a group of vents (and it is thought that convection of fluid continues within the sea-floor, even after it has moved some distance from the ridge and been covered with a layer of sediment). There is no doubt that the volume of metal-enriched rock associated with a vent field could be worth exploiting if metal prices become high enough.

Since the 1970s expedition to the Galápagos, warm-water vents, black smokers and (intermediate between the two) 'white smokers' have been found in a variety of plate-tectonic settings, including other spreading ridges and transform faults (cf. Figure 2.5).

By reference to Figures 2.5 and 2.6, can you suggest two other types of topographic features which could have hydrothermal vents associated with them?

For percolating seawater to be heated, the features would need to be volcanic in origin, with active (or recently active) volcanism. The two types of features suggested by Figures 2.5 and 2.6 are mid-ocean seamounts (the active parts of 'hot spot' seamount/island chains) and the seamounts (and islands) that make up the arcs associated with subduction zones where ocean floor is subducted below ocean floor (left-hand side of Figure 2.6).

Since the 1970s, many sites of hydrothermal activity have been discovered and investigated, both on spreading ridges/transform faults and in association with volcanic arcs (e.g. that related to the Marianas Trench; see Figure 2.5). More hydrothermal sites are being found all the time, and although there are still long segments of plate boundaries for which no hydrothermal vents have been identified, this is almost certainly because no-one has yet been there to look for them.

One of the problems that has interested people studying vent fauna is how the animals manage to spread from one vent 'field' to another, given the large distances of cold, food-poor (especially for them) bottom waters that separate one field from another. The ability to spread to other vents would seem particularly important because vents are ephemeral. As the cold, dead chimneys seen at the Galápagos indicated, vent fields do not last long on a geological time-scale. We now know that individual vents are only active for a few decades, and groups of vents only for a thousand years or so.

How do you think that vent animals can spread, given that many have planktonic larvae?

- The planktonic larvae will be dispersed in currents, and a small proportion of them will end up in the right environment.

Perhaps not surprisingly, the communities that live around vent sites on the Mid-Atlantic Ridge are distinct from those that live (say) along the East Pacific Rise. For example, tubeworms and Pompeii worms ('The Deep', sequence 11) are characteristic of Pacific vents, while a certain type of anemone (shown in Figure 10.12c) is characteristic of the Atlantic. Strangely, tubeworms like those of Pacific vents were recently found at a newly discovered vent site in the Arctic, to the north of Iceland.

10.4.2 Cold seeps and whale-falls

Cold seeps, such as that associated with the 'brine lake' shown in 'The Deep' (sequence 12), are fundamentally different from hydrothermal vents, i.e. from black smokers and warm-water vents. The sulfide issuing from hydrothermal vents, and supporting the chemosynthesis there, is formed as a result of a chemical reaction between heated seawater and hot basalt; in other words, it is inorganic in origin. By contrast, the methane that bubbles out at cold seeps originates from the decomposition of organic debris (primarily phytoplankton) which has been buried by sediment. (If such debris is buried under sufficient pressure it forms methane hydrates, which you may have heard discussed as a possible hydrocarbon fuel; sometimes it forms oil.)

The cold seep shown in 'The Deep' is in the Gulf of Mexico, where methane (and sulfide) is being produced from organic remains that accumulated in the Atlantic when it was just opening. In general, cold seeps are typically found along continental margins (shelf, slope and rise).

- Can you suggest why this might be?
- Coastal seas generally have the highest levels of primary productivity, so these are also the areas where rates of supply of organic debris to the sea-bed are greatest.

As you will now appreciate, most of the organic material that reaches the sea-bed is consumed by benthic animals, but sediment slips or turbidity currents occasionally result in accumulations of organic remains being carried further offshore and buried in oxygen-poor conditions before they can decompose or be eaten. These are the organic remains that may be converted to methane or oil.

Cold seeps, with ecosystems similar to those along continental margins (bacterial mats, mussels, clams and perhaps tubeworms), have also been found in deep-sea trenches (where organic-rich sediments are being carried down into the mantle at subduction zones; cf. Figure 2.6), in basins enclosed by island arcs, and in very shallow water. Not all are based on methane or hydrogen sulfide; some are based on tarry deposits, and others on organic-rich fluid, both of which formed from the remains of organic material, particularly dead phytoplankton. As mentioned in 'The Deep', cold-seep tubeworms can live for more than 200 years; individual cold-seep communities may last even longer.

In 2005, an expedition to study the break-up of the Larsen B Ice-shelf off Antarctica discovered a vast area of cold-seep communities (including white bacterial mats and giant clams) on the sea-bed at a depth of 850 m. Whether these communities will continue to thrive in the absence of the ice-shelf that may have been above them for thousands of years, is not clear.

In part II of 'The Deep', you saw a gray whale skeleton supporting a community of animals similar to those found around cold seeps and vents. It has been estimated that about 69 000 baleen whales die every year (many of them from starvation or disease during migration). Malnourished whales have less blubber, and so sink quite quickly; once below 1000 m depth, pressure prevents expansion of the gases produced during decomposition, so the carcases continue to sink, rather than bobbing to the surface again.

Large carcases always decay anaerobically, because their small surface area : volume ratio means that the bulk of the body cannot be reached by oxygenated seawater diffusing in from outside. In other words, the bacteria bringing about decomposition respire using oxygen taken not from seawater, but from oxygen-containing compounds making up the whale's soft tissues.

A dead whale, weighing (say) 40 tonnes, could contain as much food as would normally fall to an area of sea-bed over the course of 4000 years. It could take as long as 10 years for scavengers (e.g. hagfish, sharks, king crabs) to strip away all the soft tissue (sequence 7, part II of 'The Deep'). After that, another group of animals arrives to feed on the bones, which are 60% lipid by weight. These include writhing masses of worms (e.g. the polychaetes seen in sequence 8), and various types of molluscs, at population densities seen nowhere else in the deep sea.

Many of the animals have only ever been found on whale carcases. A recently discovered example are the so-called 'zombie worms', a few centimetres long. These extraordinary animals have 'roots' which penetrate whale bones and, with the aid of symbiotic bacteria, extract lipids from the bones. A number of very similar such worms have been found living on whale bones in widely separated locations, from the waters off California to the North Sea. They have been given the generic name *Osedax*, meaning 'bone-eating'. The visible parts of the worms are rather flower-like (Figure 10.14), and in the case of one species, the part of the worm that is exposed to seawater is covered with mucus. It has therefore been given the name *Osedax mucofloris* – bone-eating mucus flower!

After a decade or so, yet another community of animals moves in to live off the whale bones. For as long as a hundred years, anaerobic bacteria continue to break down the

Figure 10.14 A whale bone colonised by *Osedax frankpressi* worms, at a whale-fall site more than 3000 m deep in Monterey Canyon off California (photographed from the remotely operated vehicle *Tiburon*).

remaining lipids, releasing methane and sulfides that, via methane- or sulfide-oxidising bacteria, then support worms (especially polychaetes), crustaceans, limpets, mussels and clams (Figure 10.15). Of the ~ 200 species of macrofauna found on well-decayed whale bones, some are 'whale-fall' specialists, and some are also found at sulfide-rich vents, or cold seeps, or both.

(a) (b)

Figure 10.15 Photographs taken from *Alvin* of the remains of a whale (either a blue whale or fin whale) found in the Santa Catalina Basin, off California. Note that these photographs show the bones of a whale that has been on the sea-bed for about 50 years, i.e. longer than the remains shown in 'The Deep'. (a) Close-up of mussels nestling in an eroded rib-bone. The mussels are about 1 cm long and are sustained partly though chemosynthetic bacteria. (b) Vertebrae of the same whale about 20 years later. On the ends of the vertebrae (which are about 40 cm long) are numerous snails and (especially on the far bone) limpets, which are grazing on the bacterial mats and/or are sustained through chemosynthetic bacteria. In the mud can be seen the shells of clams, which are sustained through chemosynthetic bacteria. The fish, the orange anemone, the small sea-cucumber (on far left) and the crab are not specific to whale falls, but have probably been attracted to feed on the enhanced biomass. Compared with other deep-sea communities, whale-fall sites have a large number of animals, a large biomass and a high species diversity.

- Would you say that the source of energy for communities living on whale bones has more in common with the energy source at black smokers/warm-water vents, or the energy source supporting cold-seep communities?

- It has more in common with the energy source supporting cold-seep communities – chemosynthesis based on methane and hydrogen sulfide produced from organic debris which has sunk from surface waters. The hydrogen sulfide and methane emitted from black smokers and warm-water vents is produced as a result of chemical reactions between seawater and hot basalt (i.e. it is produced inorganically).

Because whale remains support a succession of different communities over such a long period, at any one time there may be more than 850 million 'active' whale-fall sites on the sea-bed (compared with perhaps 80 000 cold seep sites).

10.4.3 Is there spring at hydrothermal vents and cold seeps?

Recently, scientists studying vent fauna were amazed to discover that, like many animals of the abyssal plains, some animals living around smokers and cold seeps (including *Alvincans stactophila*, a type of shrimp living around the 'brine pool') reproduce seasonally. At first sight, it is not clear why they would do this, given that hydrothermal vent sites are oases of abundance all year round.

- Given what you read in Section 10.3, can you suggest why it might be advantageous for some vent animals to spawn seasonally?
- Some vent animals produce planktonic larvae (i.e. meroplankton). Some of these dispersing larvae will need to feed on marine snow until they find somewhere suitable to settle. (Others, such as those of tubeworms, are sustained by yolk-sacs, and so do not need to feed.)

Of course, not all vent sites are below surface waters where primary production varies seasonally (cf. the answer to Question 10.7). So far, it seems to be the case that seasonal reproduction only occurs in vent/seep animals living below seasonally varying primary production.

Postscript: Is there photosynthesis in the deep sea?

The deep sea continues to produce surprises. It has been known for some time that a certain species of shrimp, which lives close to hydrothermal vents, has a crude light-sensing organ on its back. This organ is thought to help it find food, or somehow help it avoid being scalded by vent fluids. This latter idea suggested that some vent fluids are so hot that they glow – and indeed this has turned out to be the case (although the intensity of the light is very low). This in turn raised the question as to whether the light could be used for photosynthesis – and, tantalisingly, a type of photosynthesising bacteria (known as green sulfur bacteria) has been found in water samples collected from vents. Whether the bacteria truly originated within the vents, and whether they use light produced as a result of sea-floor rock being extremely hot, is not yet confirmed – if they do, it raises possibilities about the origin of photosynthesis on Earth, and perhaps on other planets.

Question 10.8 Why do you think that cold-water corals (part II of 'The Deep', sequence 7) need to be able to capture much larger particles of food than shallow-water reef-building corals? ◀

Question 10.9

(a) As you will have seen in 'The Deep', many deep-sea fish have large eyes, despite the fact that they live way below the reach of sunlight. Why might they find good sight useful?

(b) What other senses do fish make use of? For each sense, give an example from 'The Deep'. ◀

Oceans in crisis

11

In this final chapter of the course, we will look at overfishing, thought by many experts to be the greatest current threat to life in the oceans – a threat more severe even than pollution. In studying this important topic, you will be able to apply knowledge and ideas from earlier chapters, as the fish which humans exploit are an integral part of the ocean ecosystem.

Fishing is sometimes described as 'harvesting the oceans', but the way humanity exploits the oceans today is by no means like farming. What farmer would knowingly deplete his stock without ensuring that there was a reliable supply of replacement animals? For at least 50 years, fishing has resembled hunting – not the sustainable hunting practised by, say, the indigenous population of the Amazonian rainforest, but rather the large-scale slaughter of the herds of buffalo on the North American plains. We are now paying the price, and so are marine ecosystems worldwide.

11.1 Introduction

Figure 11.1 shows how the annual global marine 'harvest' (living organisms taken from the sea) rose from 17.5 million tonnes in the 1950s to 80–90 million tonnes between 1995 and 2005. To some extent, this rise can be explained by a growth in world population from about 2.5 billion people to about 6 billion over the same period, but an increase in the number of mouths to feed is only part of the story. We'll look at the factors which led to such a dramatic increase in marine catches shortly; but first, you may find it useful to remind yourself about where good fishing grounds are likely to be found, and why.

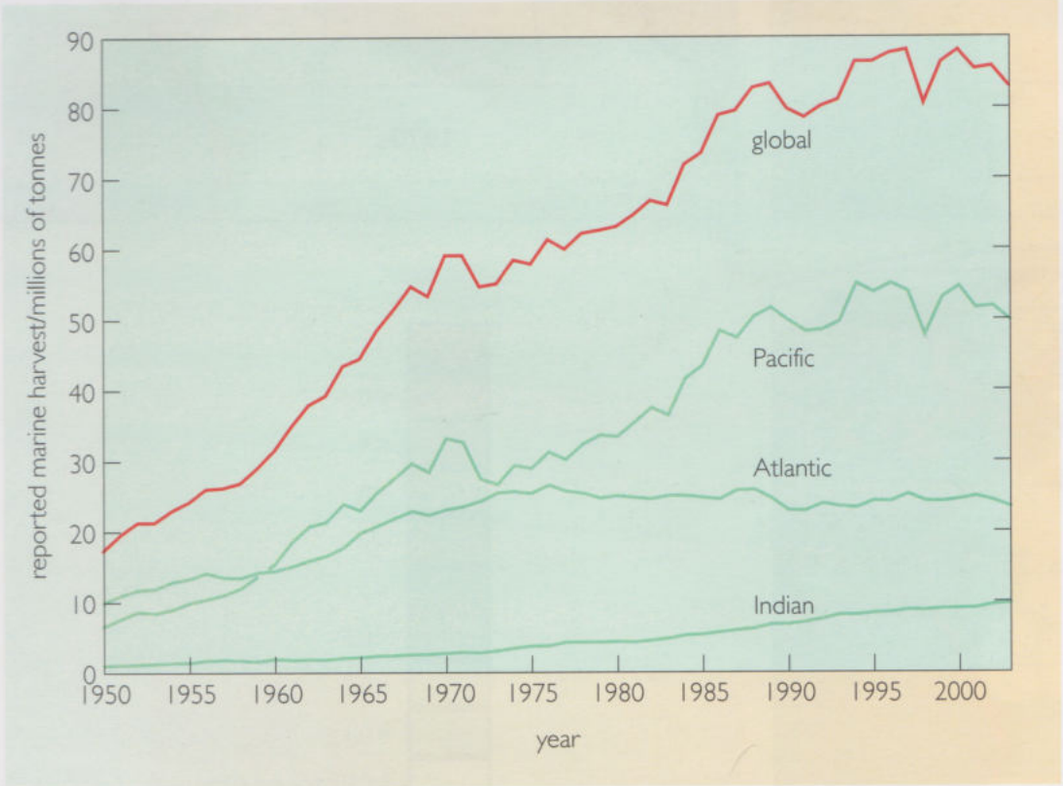


Figure 11.1 *Uppermost plot:* Annual global marine harvest, as reported from 1950 to 2004, in millions of tonnes (i.e. megatonnes, Mt) per year – mainly fish, but also marine mammals, crustaceans, molluscs and a relatively small contribution from marine plants. *Lower three plots:* Data for the three ocean basins; data for the Southern Ocean (around Antarctica) are not included but the catch is too small to show clearly on the scale of the vertical axis. (*Note* These plots are based on data reported by individual countries, and are subject to a high degree of error; e.g. it is thought that over recent decades China may have exaggerated its annual catches by perhaps 5–10 Mt. As you will see, obtaining accurate information about fish catches is fraught with difficulty.)

The Pacific is roughly twice the area of both the Atlantic and Indian Oceans, so it is perhaps not surprising that it yields by far the largest fish catch. However, although the Atlantic Ocean is only a few per cent bigger than the Indian Ocean, its fish catch is 2–3 times greater.

By reference to Figure 4.1, can you suggest why this might be?

Like the Pacific, the Atlantic has large areas with high primary productivity, particularly at mid- to high northern latitudes, where winter mixing brings nutrient-rich water to the surface (Section 4.3). High primary productivity means more biological production at higher levels in the food chain, and so greater production of fish. The Indian Ocean, by contrast, is a largely tropical ocean, where high productivity is confined to areas of upwelling (Section 5.2.1).

As you are probably aware, overfishing is a global problem, but for much of this chapter we will be concentrating on the Atlantic because it has the longest recorded history of exploitation and is the best studied. Figure 11.2 shows catches of commercial fisheries in the North Atlantic, averaged for the decades of the 1950s, 1970s and 1990s. Forgetting the differences between the three maps for the moment, study the general patterns they show and answer Question 11.1.

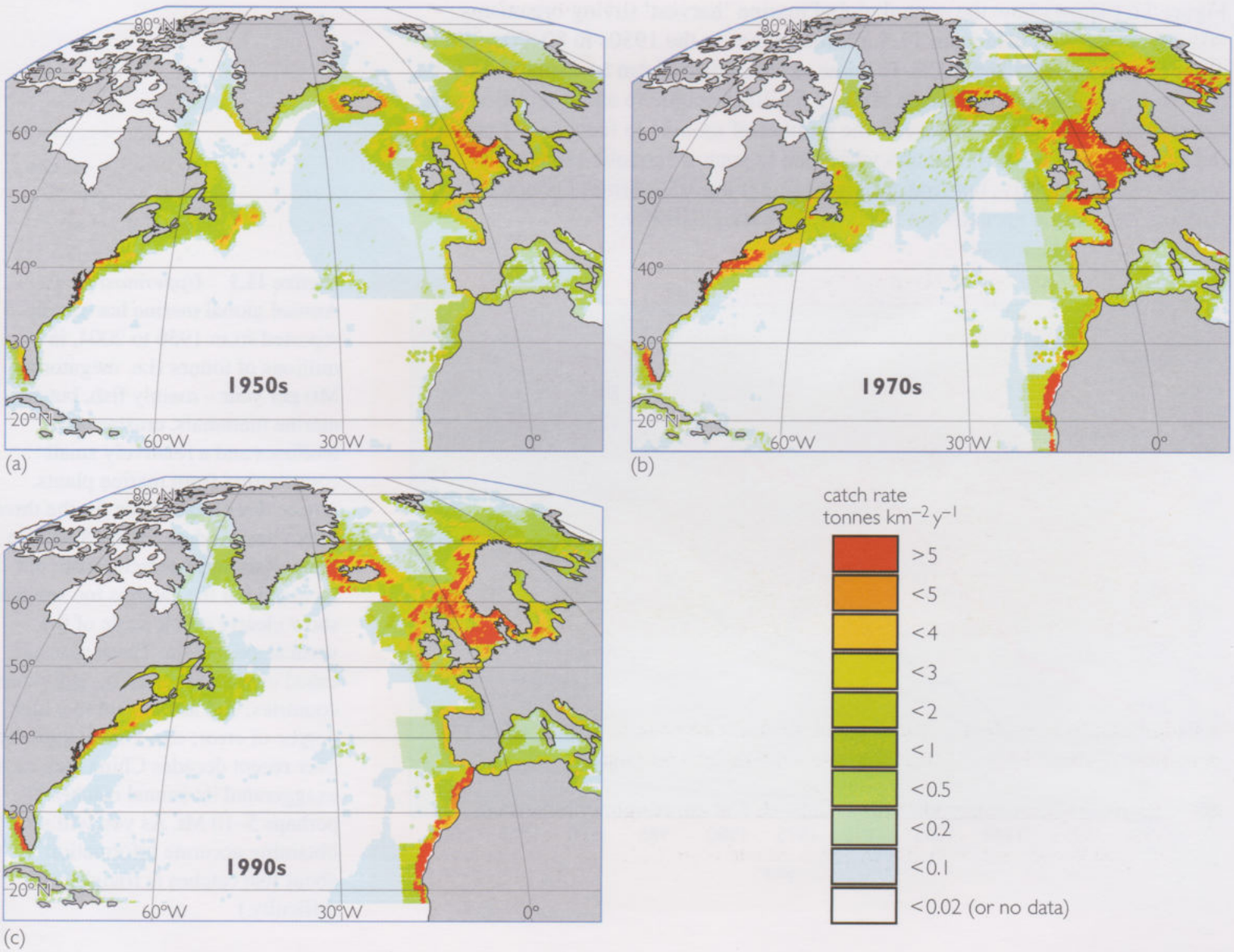


Figure 11.2 The distribution of weight of fish caught annually per square kilometre by commercial fisheries in the North Atlantic and adjacent seas (in tonnes km^{-2} y^{-1}), averaged for the decades of (a) the 1950s, (b) the 1970s and (c) the 1990s. (*Notes* The 'hot spot' to the south of Iceland and west of the British Isles corresponds to fishing grounds associated with the Rockall Bank. The straight edges to some areas of colour must reflect the way in which the data have been collected.)

Question 11.1

(a) How would you summarise which general areas tend to yield a low fish catch (white and pale blue) and which tend to yield a high fish catch (green, orange, red)? How do food chains in the two types of area differ from one another? (*Hint:* Look at Figure 2.4 and think back to Section 5.5.)

(b) What is the particular reason for the areas of very high fish catches off the west coast of Africa (in the 1970s and 1990s)?

(c) By reference to Figure 4.1, can you suggest some other regions of the Atlantic, to the south of the area covered by Figure 11.2, where you would also expect fish catches to be relatively high? (Try to think of *at least two* different areas.) ◀

The maps in Figure 11.2 were compiled by combining data on catches of different fish species with information about the spatial distribution of those species. Determining the distribution of a given species is not straightforward because, as you know from Section 9.2, fish undertake migrations as they grow to maturity, and over the course of their breeding cycle, so at different times during their life-cycle they are found in different depths and at different distances from the coast. As an example, Figure 11.3 shows why the life-cycle of the Atlantic cod means that it moves back and forth across the continental shelf over the course of its life (the diagram ignores the fact that cod also move *along* the coast).

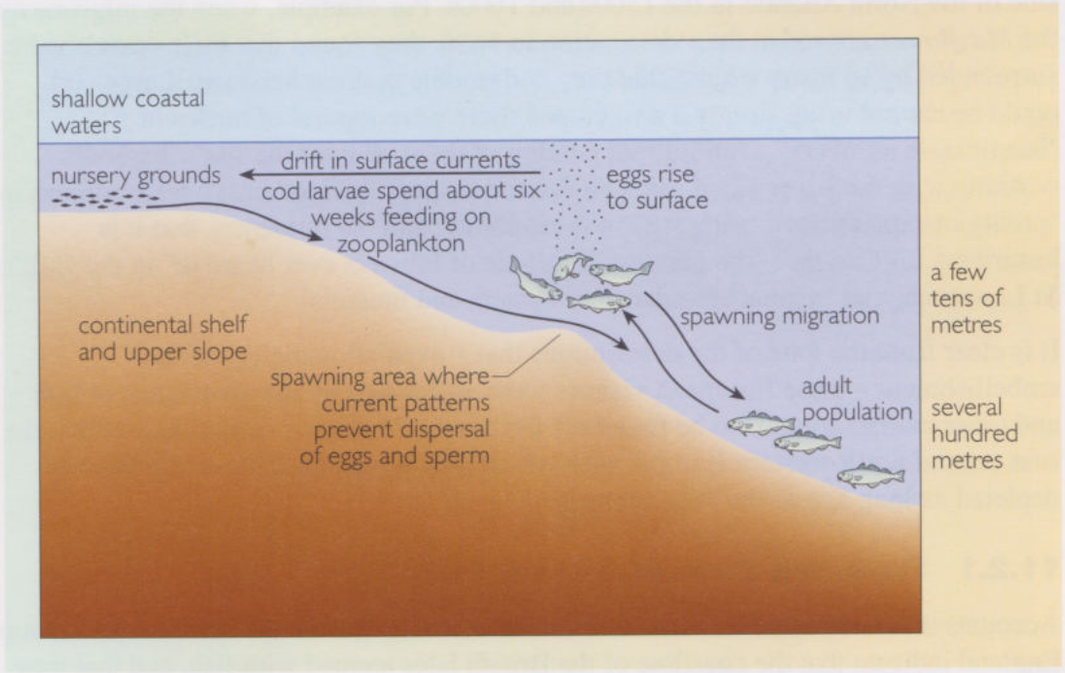

shallow coastal waters
nursery grounds
drift in surface currents
cod larvae spend about six weeks feeding on zooplankton
eggs rise to surface
spawning migration
continental shelf and upper slope
spawning area where current patterns prevent dispersal of eggs and sperm
adult population
a few tens of metres
several hundred metres

Figure 11.3 Highly schematic diagram showing the life-cycle of Atlantic cod (*Gadus morhua*) in relation to depth and distance from the coast. Atlantic cod live over the continental shelf and upper continental slope off Newfoundland (the Grand Banks etc.) and New England, off southern Greenland, around Iceland, as well as over much of the continental shelf of north-western Europe (the Baltic, North Sea, Irish Sea, English Channel etc.) and the Barents Sea. Within these areas, there are numerous spawning grounds.

As adult cod live and feed at the sea-bed, or fairly close to it, they are described as *demersal*; in the USA and Canada, demersal fish are known as 'groundfish'.

Can you suggest some other demersal fish that are caught commercially?

The best known are probably plaice, sole and other flatfish.

11.2 A short history of (over)fishing

In studying Figure 11.2, you may well have been assuming that the map for the 1950s represents a time when, though exploited, the oceans were in a more or less 'pristine' condition. However, as you will see, this was by no means the case.

Figure 11.2 is taken from *In a Perfect Ocean: the state of fisheries and ecosystems in the North Atlantic Ocean,* written by Daniel Pauly and Jan Maclean, and first published in 2003. This book is an accessible account of the findings of a project* to investigate the effect of fishing on the ecosystems of the North Atlantic. It presents revealing data collected during the project, some of which we will reproduce later.

Although in some ways *In a Perfect Ocean* only confirms what has been known for some time – i.e. that the waters of the North Atlantic are grossly overfished – in other ways its content is quite shocking. A fundamental point made most forcefully by the authors is that each generation considers that most of the progressive degradation of marine communities has occurred over the course of their own lifetime, and that the seas of their youth represented a more or less 'pristine' situation. This means that reminiscences by old seamen of larger fish and greater abundances in the time of *their* youth are (wrongly) always assumed to be exaggerated 'fishermen's tales'. More seriously, it means that current conditions are always measured against a baseline that is continually shifting, so that the true extent of decline is never fully appreciated.

A more accurate picture of the abundance of marine life to be found when seas were not overexploited is provided by accounts of Europeans who voyaged to the western side of the North Atlantic in the 1500s and 1600s. For example, when the pilgrims on the *Mayflower* arrived at their destination in 1620, they found that their vessels were surrounded by so many whales that they had trouble making headway. Large cod could be caught using simply a basket, and there were reports of turtles in 'inestimable numbers, … an infinite number of them all over the sea'; 'harbours writhing with the silver-sided splashing of the stripers' (striped bass); huge salmon in 'prodigious quantities'; 'sturgeons in great plenty' and 'so numerous that it is hazardous for Canoes'; 'the greatest multitude of lobsters ever heard of' in the Gulf of St Lawrence; and 'a great abundance of oysters and mussels'.

It is clear from the tone of the descriptions that – even allowing for some embellishment – these European visitors were astonished by the abundance of fish and other marine animals to be found off the coast of America. This suggests that the seas around north-western Europe, with which they were familiar, were relatively depleted as long ago as the 16th century.

11.2.1 From fish traps to factory ships

Accounts that have come down to us from the centuries before the Norman invasion of England indicate that the coastline of the British Isles teemed with fish, and that they were readily caught in various kinds of traps (see Figure 11.5a) across estuaries and around the coast. In mediaeval times, the most important fisheries in European waters – particularly the North Sea and the Baltic – were those for herring. One of the most lucrative herring fisheries was along the Baltic coast of south-western Sweden; it was said that in the 14th century this area was so rich in herring that 'they could be caught with the hands, and it was almost impossible for a boat to make its way through the dense masses of fish'; in the autumn fishing months, 60 000–70 000 extra people would come to this coastline. However, the herring came to be known as 'fickle', and

*The project was named 'The Sea Around Us', after Rachael Carson's influential book of the same name. It began in 1999, and is still continuing.

from time to time over the following centuries, herring populations would suddenly disappear from one location, and reappear elsewhere. So important was the trade in herring – a staple food for rich and poor alike – that the movement and fluctuating abundances in herring populations led to a succession of shifts in wealth and political power in the region, as the Danes, the Dutch and the Swedes in turn dominated the Baltic fishery. Over the same period, other populations of herring brought wealth first to Norway, then to Scotland, Germany and, more recently, England.

From about 1870 onwards, there was large-scale introduction of steam-powered fishing vessels (the largest with powered trawl winches) and sea fisheries began to expand rapidly. Voyages to distant fishing grounds were further encouraged by improvements in methods of preserving the catch. Drying and salting had been used to preserve fish at sea since the Middle Ages, and natural ice had been imported from countries such as Norway. Now, however, every major fishing port had a mechanical refrigeration plant which supplied ice to vessels beginning their outward journeys, and later also provided ice to keep fish cold while in transit by train to the larger cities. During the 1930s, certain high-value fish were actually frozen at sea, and as the technology improved, complete catches were being frozen and transported from distant fishing grounds with minimal loss of quality.

In Britain, early indications of a decline in catches were noted before the First World War, and again in the 1930s. The Second World War provided a respite for fish stocks, as most trawlers were diverted to war purposes (and many were sunk). However, the temporary lull was more than compensated for by a number of technological developments arising out of the war, notably in sonar, electronics, navigation, and acoustic fish-finding systems. In addition, there were new refrigeration techniques and developments in catching gear and nets (cf. Box 11.1). The first fish factory processing trawler (designed on the experience of the Antarctic whaling industry) was completed in Aberdeen in 1954, and its design was immediately copied by the Soviet Union and other eastern bloc countries, and Japan; to a lesser extent, these trawlers were also commissioned by the UK and other European countries, which already had large numbers of conventional trawlers capable of voyaging to distant waters. Most UK ships operated out of Hull and Grimsby, working mainly in the northern Atlantic and Arctic waters, close enough for them to bring back good quality 'iced fish'. Today, such vessels often return with their holds full of ready-packaged frozen fish fillets.

- On the basis of the areas where the catch rate exceeded 0.2 tonne km^{-2} y^{-1} (green, orange and red in Figure 11.2), would you say that the effects of developments like those discussed in the previous paragraph can be seen in the first two maps in Figure 11.2?

- Yes. In the 1950s, areas with high catch rates were generally fairly close to land, and only extended significant distances from the coast over continental shelves. By the 1970s, catch rates over continental shelves had increased, and a large part of the north-eastern North Atlantic was being significantly exploited. There were also various 'fishing hot spots' in mid-ocean, particularly to the east of Canada and in the waters to the east of Greenland. (In addition, large fish catches began to be taken off West Africa.)

Factory trawlers are sometimes erroneously referred to as 'industrial trawlers'. However, industrial fishing (i.e. taking fish for use in industry, rather than for direct human consumption), is often undertaken by fairly small vessels, and involves catching small (mostly pelagic) shoaling species such as anchovy and herring, as

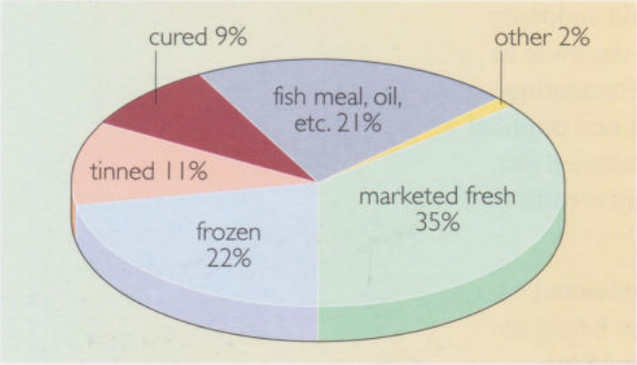


Figure 11.4 How the annual global aquatic production of about 150 Mt is used, according to data published in 2000. The total includes both marine and freshwater catch, and aquaculture production; in 2003, the catch in inland waters was ~ 9 Mt, and aquaculture produced ~ 55 Mt.

well as sand-eels (particularly in the North Sea). These are either pumped on board and then sieved out, or caught in trawls. Over half the global catch by industrial fisheries is converted to fishmeal and fish oil (Figure 11.4), which are used for feeding terrestrial and aquatic livestock, such as pigs, poultry and farmed salmon (see Section 11.6.1), and for fertiliser. Fish oil is also used in margarine, paint, shoe polish and varnish, and in the pharmaceutical industry. In the past, it has even been used as fuel for power stations.

According to Figure 11.4, approximately what percentage of global fish production is used directly as food for humans?

The answer must be 35% + 22% + 11% + 9%, i.e. about 77%.

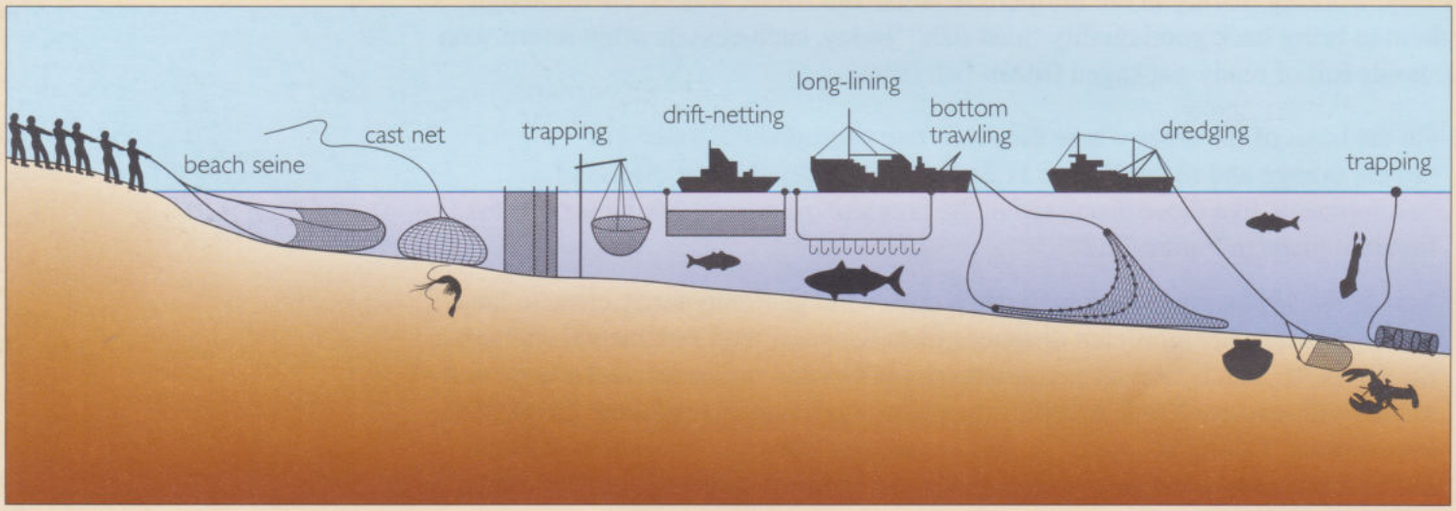
Much of the remaining ~ 23% contributes to human food supplies indirectly: we will look at whether this makes ecological sense in Section 11.6.1.

Box 11.1 Methods used in commercial fishing

Figure 11.5 illustrates the main techniques used in commercial fishing. It is by no means comprehensive, and is simply intended to convey the range of techniques and equipment used to catch fish, from shoreline to mid-ocean, and from surface waters down to the continental slope. The silhouettes represent just some of the animals targeted by the various methods: also, some fish are targeted by different methods in different parts of the world. The methods illustrated fall into the following categories: trapping, dredging, 'hook-and-line', entangling (gill nets and drift nets), encircling (purse-seining) and trawling. Trapping and dredging are used only in shallow coastal waters (including estuaries); the other methods are used in waters of all depths.

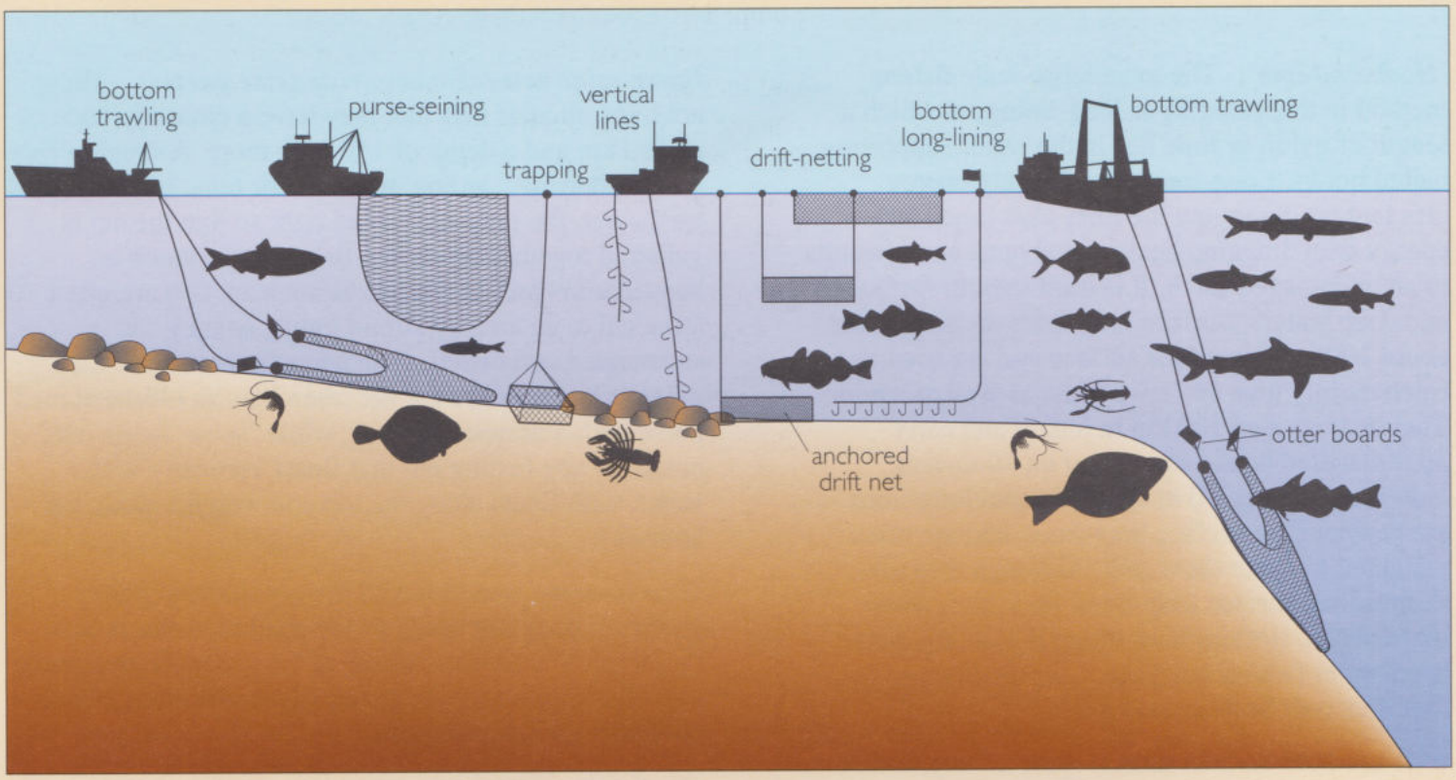
Trapping Many types of trap are used to lure fish or crustaceans into a confined space from which they cannot escape. In the waters around the British Isles, the lobster pot (far right of Figure 11.5a) is the most commonly used trap, but there are many ingenious designs (e.g. left side of Figure 11.5a).

Dredging Dredges are used to collect crustaceans and molluscs (e.g. tiger prawns and scallops), and work by digging into the sea-bed and scraping up the shellfish (and any other animals present).

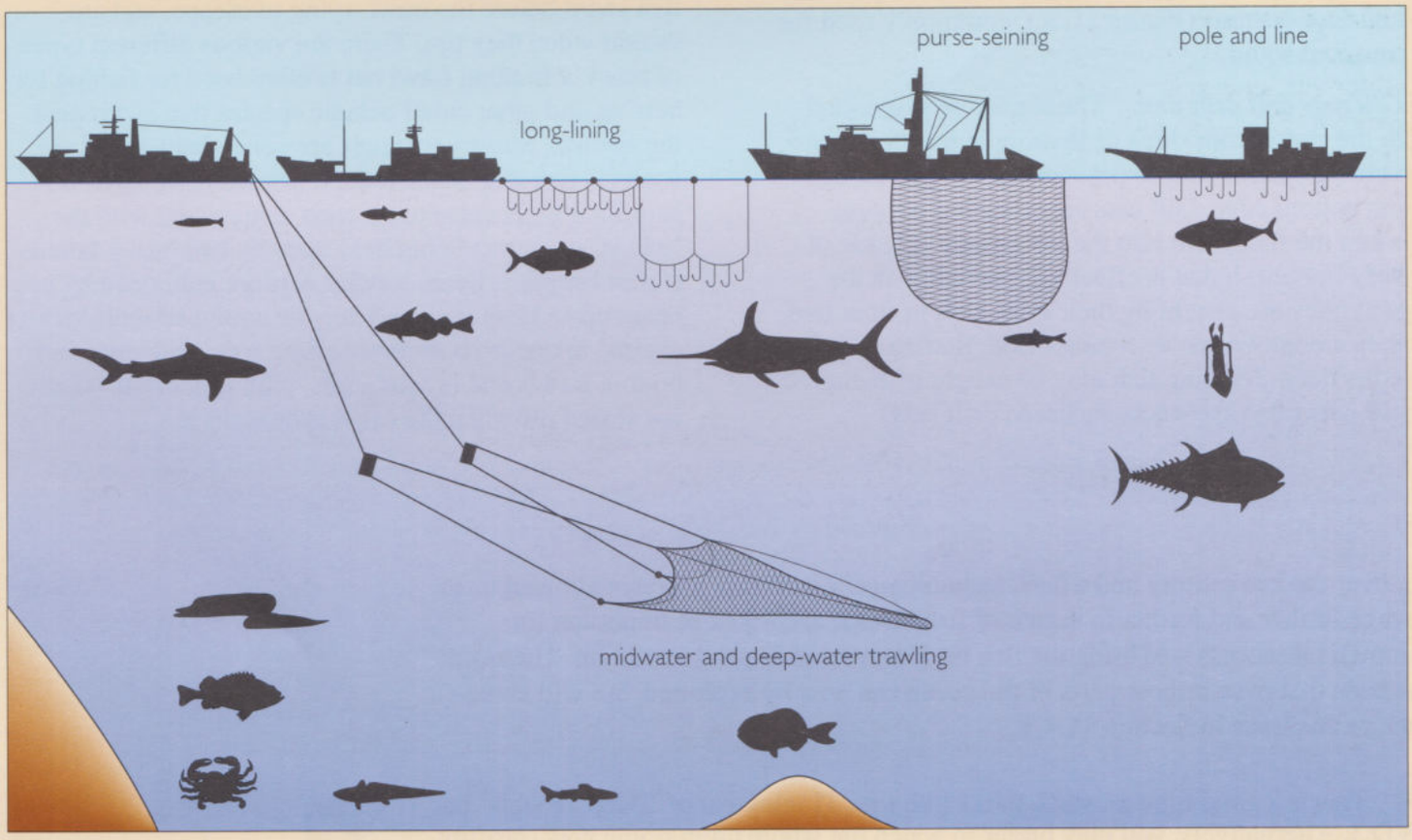


(a) shallow coastal waters

Figure 11.5 Highly schematic diagrams to show the principal techniques used in commercial fishing: (a) in coastal waters; (b) over the continental shelf; (c) in the deep ocean. The silhouettes of fish etc. show some of the species targeted by the various methods. (You do not need to remember the details of this diagram.)



(b) continental shelf and slope



(c) deep water

'Hook-and-line' The most large-scale fishing method in this category is long-lining, in which a length of nylon or rope lies in the water supporting baited hooks. Long-lining is relatively energy efficient, as deploying the lines uses much less energy than dragging heavy trawl nets, and it results in an undamaged catch. It is used in both surface and deep waters. Surface long-lines are suspended about 200 m beneath the surface and are used to catch mainly tuna and swordfish, as well as squid. They may exceed 100 km in length and carry 30 000 baited hooks suspended on 40 m-long 'sub-lines' spaced 50 m apart. Bottom long-lines are heavier than surface long-lines, and are often weighted to make them sink. Although they are shorter than surface long-lines, they carry many more hooks. Bottom long-lining is used to catch deep-water fish such as ling, hake and Patagonian toothfish (see Section 11.4.3).

Also used are vertical lines (Figure 11.5b), which are often used to catch squid. Vertical lines may be deployed to reach down into gaps between rocks. There are also automated or hand-operated pole-and-line systems (Figure 11.5c), commonly used for tuna and squid.

Gill nets and drift nets These may be suspended in the water from ships or floating buoys, forming a vertical curtain held in position by weights along the bottom edge. Gill nets are so-called because when the fish swim into the net (which is made of very fine mesh that is effectively invisible in the sea), they are caught by their gills. Left to float free, they are known as 'drift nets'. Cod, flatfish and other deep-dwelling fish may be caught in anchored gill nets (also known as anchored drift nets).

Purse-seine nets (also known as seine purses) These are huge circular nets that may have a circumference of up to 1 km and a depth of 150 m or more. A shoal of fish such as herring, sardine, mackerel or tuna, is surrounded by the net, the lines are pulled tight so that the net is gathered together below the fish, and the catch is heaved on board. In the Mediterranean, fish are often attracted to an area by strong lights, so they can be surrounded and netted. (The name 'purse-seine' was given because in use the net resembles an old-fashioned purse with a drawstring neck, while 'seine' is the old name for any fishing net that floats vertically in the water, with floats along the top and weights along the bottom.)

'Beach seines' are deployed in very shallow water; another type of net used in very shallow water is cast (i.e. thrown) onto the surface of the water (often from a small boat); after the weighted edges sink, they can be tightened with a drawstring.

Trawl nets Trawl nets are pulled through the water at different speeds depending on the type of fish being hunted, and are hauled in using powerful winches. The fish swim before the trawl trying to escape, and are caught when they tire. There are various different types of trawl: a floating trawl net is often used for fishing for herring and other small pelagic species that swim near the surface. Midwater trawls are cone-shaped, and are used for fish that swim at depths down to about 500 m. Bottom trawlers also use a cone-shaped net, with the 'wings' of the net being held open by two heavy boards ('otter boards'). Beam trawler nets are held open by a beam up to 12 m long and may be equipped with 'tickler chains' to disturb bottom-dwelling fish. Midwater and bottom trawls end in 'cod-ends' with fine mesh, which are closed off when the catch is brought in.

So, over the last century and a half, technological developments have allowed us to voyage further and further in search of fish stocks, and – just as important for commercial success – to bring the fish back to market in good condition. The result has been that even remote parts of the ocean can now be exploited. We will come back to this issue in Section 11.4.3.

▶▶ This is a good time to watch part I (the first 35 minutes) of 'Deep Trouble' on DVD 3. Alternatively, you may prefer to watch the whole programme now (bearing in mind that the notes for parts II and III are later in the chapter). ◀◀

Notes on 'Deep Trouble, (part I)

General notes This programme was first broadcast in 2001, since when the state of global fisheries has further declined.

You will be familiar with the scientific background to much of what is shown in this programme, so we are not providing many notes about specific sequences.

You may find some of the material shocking.

Sequence 2 CITES is the *Convention on International Trade in Endangered Species*. Appendix 1 relates to species threatened with extinction.

Sequence 3 John Shepherd refers to 'heavy fishing pressure by purse-seiners'. This is the expansion in the 1960s of purse-seine fishing (cf. Figure 11.5, Box 11.1) north and west of the Shetlands, to target stocks which had previously been only lightly fished. This expansion was made possible by the introduction of power blocks (powered pulley systems) which allowed large purse-seine nets to be used in the open ocean. A similar expansion occurred in the Norwegian purse-seine mackerel fishery.

11.2.2 By-catch and discarding

The following account comes from a pilot in the Royal Canadian Air Force, who used to fly over the Grand Banks area of the North Atlantic in the 1950s:

> One morning we raised forty or fifty paired Spanish draggers working Green Bank (Grand Banks area) … some of them seemed to have a tail … when we came over them at about 2,000 feet, we saw that it was dead fish. There must have been millions of them stretching out astern of each boat that had just hauled its net and was sorting the catch on deck. Undersized fish were going over the side like confetti.
>
> F. Mowat (1984) *Sea of Slaughter*, quoted in *In a Perfect Ocean*.

The excessive waste associated with commercial fishing has not declined since the 1950s, although, as you saw in sequence 9 of 'Deep Trouble', the reasons have changed somewhat. In fisheries around the world, enormous numbers of unwanted fish and invertebrates are thrown back into the sea dead or dying. Appreciable numbers of mammals, seabirds and reptiles (mainly turtles) caught by accident are also discarded, generally dead. Such animals are referred to as 'by-catch'. Most are species that have no commercial value or individuals of target species that are too small to be landed, either because they will fetch a poor price or because they are below the minimum legal landing size (see Section 11.3.2).

In Figure 11.6 (overleaf), the grey segments of the bars correspond to the estimated by-catch associated with the global annual marine catch between 1950 and 1999; also shown are estimates of the weight of catch which was never reported, as well as how the reported annual catch broke down in terms of types of fish etc. The weight of fish discarded annually seems to have remained fairly constant from the mid-1980s until 1999, and it is still similar to this now.

According to Figure 11.6, approximately what weight of fish was discarded annually during this period? Without doing any detailed calculations, estimate what percentage of the *total* weight of fish landed was being discarded. (For the purposes of the exercise, ignore the catch that was not reported.)

By comparison with the vertical axis, the grey segments of the columns for 1985 onwards correspond to about 30 million tonnes. Just by comparing their lengths with the lengths of columns corresponding to the total recorded catch, we can see that about *a quarter* of the catch was being discarded.

In some circumstances, discard rates can be much higher than this, perhaps exceeding 75% of the catch, by number of individuals (cf. Figure 11.7). Often, this occurs when there has been a good breeding year but the fish are still too small to be landed. Sometimes, however, large quantities of good-sized commercially valuable species are discarded: this can happen either when quayside prices are particularly low – you saw an example of this in 'Deep Trouble' (sequence 4) – or, more commonly, when a vessel has already taken its permitted quota of a particular species and is legally prohibited from landing any more.

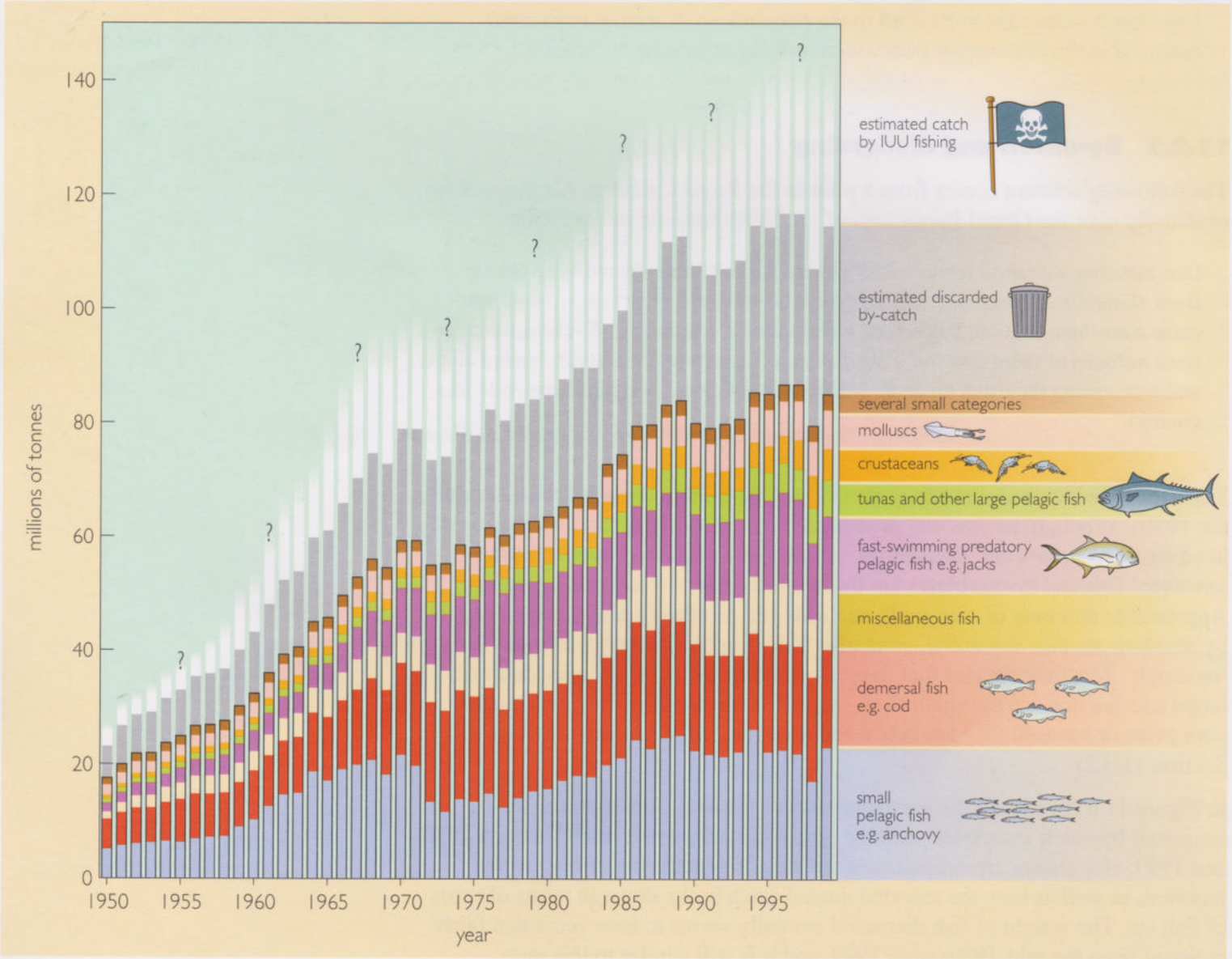


Figure 11.6 The global world marine catch for the years 1950–1999, broken down into categories. Also shown are estimates of the weight of fish discarded (grey), and the weight caught but not reported (white); this is known as illegal, unreported and unregulated (IUU) fishing (see Section 11.3.5).

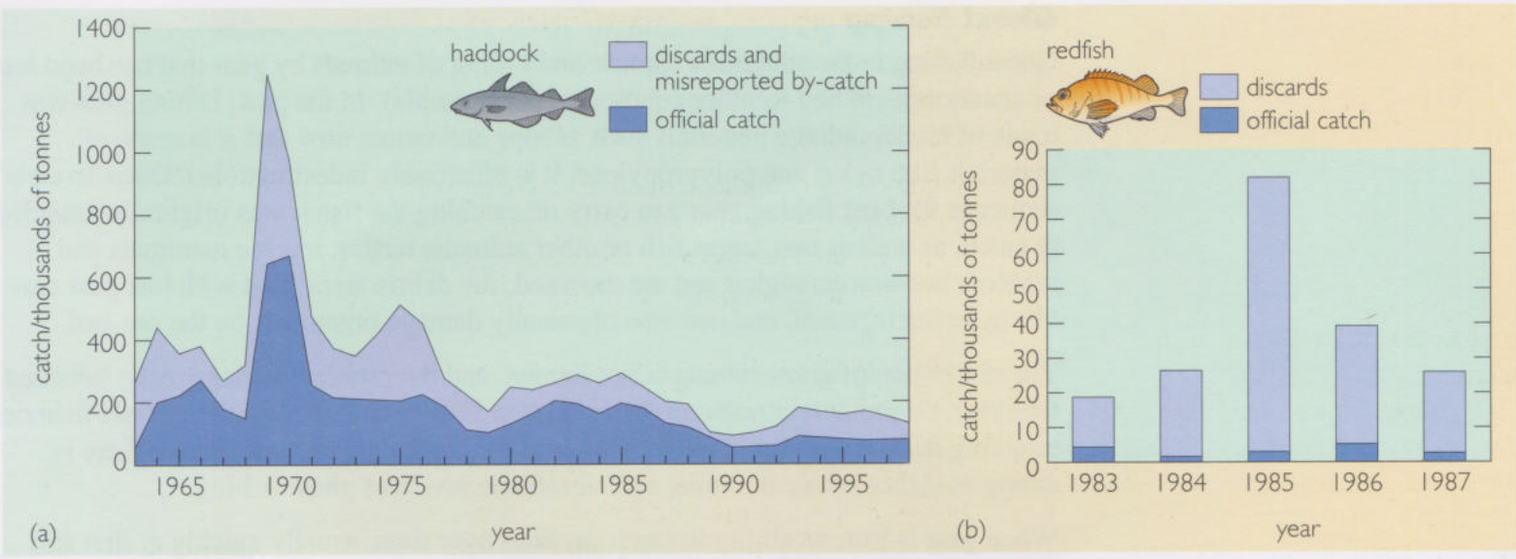


Figure 11.7 Two typical examples to show what proportion of the total catch is discarded by-catch: (a) haddock discarded in the North Sea, in fisheries from over 15 countries; (b) redfish (also known as 'ocean perch') discarded in the Barents Sea, by Norway and the former Soviet Union.

Fishing methods differ significantly in the amount of by-catch they lead to. Long-lining is sometimes described as 'species specific', but this is not always the case; for example, 90% of the *landings* of the long-line fishery off southern Spain is by-catch. Worse, the reported by-catch does not include the large numbers of animals that are thrown back into the sea; these include numerous sharks, which are usually de-finned before being dumped (shark-fins are a delicacy in Asia).

Long-lining is also responsible for the deaths of large numbers of seabirds, particularly albatrosses which are caught and drowned when they dive for the bait. On the positive side, various measures have been devised to discourage birds from diving for the bait; these include weighting lines so they sink quickly, attaching multicoloured streamers to the lines to frighten the birds off, and setting lines at night. In the case of turtles, which are also caught on long-lines, new designs of hooks are being introduced that could prevent them from taking the bait. These measures to protect seabirds and turtles have cost implications, so they will only have a significant effect if there is the political will to ensure that they are widely introduced.

Fishing with nets relies on mesh-size to determine the minimum size of fish that are caught, and larger fish and sea-mammals can often escape through openings or special panels built into the net. These and other 'technical' measures help to limit by-catch, sometimes dramatically ('Deep Trouble' sequence 9), but there is always likely to be a problem when different species of fish, of different sizes, are being targeted at the same time.

Drift nets are notorious for their enormous by-catch. They consist of strings of vertical nets, as much as 80 km long, which drift with the current. After vigorous campaigns by bodies like WWF (formerly known as the World Wide Fund for Nature), there was a worldwide ban on large-scale drift-netting in 1993, but nets 2.5 km long were still allowed). So drift-netting continues, and is a common component of European Union fleets (see Section 11.3.3).

Question 11.2 Not all animals killed or injured as a result of fishing activities are necessarily included in the statistics for 'discarding', as they are never taken on board. Thinking back to part I of 'Deep Trouble' (and Box 11.1 on fishing methods), can you suggest other types of 'collateral damage' to marine life, and marine ecosystems, which we have not mentioned so far? ◀

Ghost fishing

Ghost fishing is the continued capture and killing of animals by gear that has been lost or abandoned (in bad weather conditions, for example). In the past, fishing gear was made of biodegradable materials such as rope and twine; now that it is made of materials like nylon and polypropylene, it is effectively indestructible ('Deep Trouble', sequence 9). Lost fishing gear can carry on catching the fish it was originally intended to catch, as well as non-target fish or other animals; turtles, marine mammals and seabirds become entangled and are drowned; the debris associated with lost gear can kill by being ingested, and can also physically damage organisms on the sea-bed.

The real extent of ghost fishing is not known, and the problem varies greatly between fisheries. Of greatest concern in the context of European fleets are the gill-net fisheries targeting deep-water shark and monkfish in the north-east Atlantic, where there is strong evidence of net-dumping and significant levels of ghost fishing.

When gear is lost, its ability to catch declines over time, usually quickly at first and then more slowly. In shallow tidal waters, where currents are strong and variable, lost nets get rolled up and tangled together, and so can stop catching within a few months; over time, fouling by marine organisms also makes them more visible and less of a danger. However, gear lost or discarded in deep water with weak currents can continue 'fishing' for years.

11.2.3 Fishing and the Law of the Sea

Until the 20th century, the seas were used for fishing, trade and communication (and warfare) by a very small world population, so there was little need for nations to devise laws to protect themselves from the activities of other states. However, since at least the late 13th century coastal states have regarded the waters adjacent to their coastlines as 'theirs', so giving rise to the idea of territorial waters or *territorial sea*, outside of which lie the *high seas* (i.e. international waters).

Local laws grew up in an *ad hoc* way, as various states sought to protect valuable resources (e.g. rich shellfish beds) from exploitation by foreign states; coastal states exploited only nearby waters, so there was little need for international laws. However, by the 1500s, the Portuguese and other Europeans were fishing for cod over the Grand Banks off Newfoundland; and by the 18th century, American whalers were to be found over much of the world's oceans.

The first official attempt at codifying a global Law of the Sea was undertaken by the League of Nations in 1924. After nearly 60 years of debate and wrangling, and intermediate legal conventions, the *United Nations Convention on the Law of the Sea* (UNCLOS) was opened for signature in 1982. It eventually came into force in 1994, but – significantly – is not binding on states that have not ratified or acceded to it (which includes the United States of America).

The concept of an exclusive fishing zone – a strip of sea beyond the territorial sea in which the coastal state has complete control of fish stocks – was initially an expansion of the idea of territorial waters. A nation declaring such a zone would not generally wish to have exclusive rights to the fish in the zone, but would allow others to fish there under licence (usually within a quota system).

As recently as 1972, the great majority of states favoured a fishing limit (i.e. territorial sea plus exclusive fishing zone) of 12 nautical miles (n.m.).* However, a state's

* A nautical mile (n.m.) is the unit of lateral distance used in international treaties etc. relating to the Law of the Sea; it is longer than the statute mile used on land, and is equivalent to 1.852 km. By definition, 60 n.m. = 1° of latitude.

attitude to fishing rights reflects the importance of fishing to its economy, and the geographical location of its traditional fishing grounds – as well its political and economic power. During the 1970s, Iceland, Norway and the USA all increased their fishing limits to 200 n.m.; in the case of Iceland, this led to the 'Cod Wars' with Britain in the mid-1970s, when Iceland, fearing for the state of 'its' cod stocks, was willing to use force to prevent British vessels fishing for cod within its 200 n.m. limit. In 1977, the European Economic Community (in which negotiating rights for all member countries were vested in 1976) introduced its own 200 n.m. fishing limit.

A number of countries still have exclusive fishing zones (e.g. the UK still maintains a 200-mile exclusive fishing zone around the Falklands), but under the terms of UNCLOS such zones have effectively been replaced by *exclusive economic zones*, commonly referred to as EEZs. Within its EEZ, which extends out to 188 n.m. beyond a 12 n.m. territorial sea, a coastal state is accorded 'sovereign rights to conserve, manage, explore and exploit' all living and non-living resources in the water, and on or under the sea-bed, and has exclusive jurisdiction over all activities relating to those resources.

The legislation relating to EEZs makes it clear that states are intended to play a role in conservation as well as exploitation. There are jurisdictional controls relating to scientific research and preservation of the environment, and states are legally bound to cooperate in the conservation of highly migratory species, including marine mammals.

11.3 Why marine fish stocks are so difficult to manage

The term 'fish stocks' refers to fish populations that we exploit, and 'stocks' somehow conveys that there are large supplies of fish available for us when we want them. Increasingly, this is not the case, and it is becoming very clear that good management of a fish stock must mean employing measures that will allow the population to be exploited *sustainably*, i.e. in such a way that the population does not decline; indeed, many experts now believe that in a large proportion of cases, the aim must be to allow the population to *rise*, even if that means not exploiting it in the foreseeable future.

It is not surprising that marine fish stocks are hard to manage, given that fish are wild animals living out of sight in a largely inaccessible environment, our understanding of which is limited. To have a chance of determining the best management measures, we need to have a good idea of the 'health' of the fish stock; however, as emphasised at the start of this chapter, the baseline against which we are measuring has shifted so much that we are no longer sure what a healthy stock would be.

Even accepting that we can only work from where we find ourselves, fishery scientists still face the fundamental problem of obtaining accurate information about weights, numbers, sizes and ages of fish caught by commercial fisheries, from which the health of stocks might be deduced. National governments spend large amounts of time and money on collecting this information, but it is extremely difficult to obtain accurate statistics in those parts of the world where fishing is carried out by large numbers of small vessels landing their catches at many small harbours (artisanal fisheries). Even in more highly developed areas, the official statistics that form the basis of scientists' calculations can be seriously in error if many hard-pressed fishing skippers, faced with large bills for wages, nets and fuel, attempt to increase their earnings by misreporting what they have caught and where they caught it, or by selling fish through unofficial channels (so-called 'black' landings).

In the next section, we will look at the situation in the North Sea and adjacent areas. Fish stocks here have been studied more intensively, and for longer, than those in any other part of the world, and fishery scientists have been providing management advice to national governments and the European Union (EU) for many years. Despite the availability of so much scientific expertise, the sizes of many fish stocks in European waters are declining rapidly.

11.3.1 The fishing crisis in European waters

Until relatively recently, fishing vessels from the UK and other European countries would work in the waters in the northern Atlantic and sub-Arctic, around Greenland and Iceland (Section 11.2.1). With the introduction of EEZs from the 1970s onwards (Section 11.2.3), fishing pressure on European waters increased dramatically.

Over 30 species of fish can be caught in the North Sea, but in terms of weight, commercial catches are dominated by herring, mackerel, haddock, cod (i.e. Atlantic cod), Norway pout, sand-eel, whiting and plaice. About 50% of fish landings from the North Sea are of 'industrial' species, mainly sand-eels (Section 11.2.1). Most of the species exploited exist as a number of separate subpopulations, which occupy overlapping areas, each centred on a different spawning ground. Different subpopulations of a species (i.e. different stocks) do not necessarily prosper and decline together (remember the role of different herring stocks in the fortunes of European powers, discussed in Section 11.2.1).

Wild fish have surprisingly long natural life-spans. In the absence of fishing pressure, North Sea cod, haddock, hake, whiting and herring would live for 10–15 years or more, and plaice can live for 30 years. Different species mature (i.e. become old enough to breed) at different ages. For example, whiting mature at age two years, haddock at three, and cod at four.

In terms of their ability to produce young, what is the implication of the fact that most fish in the North Sea are killed before they are 4–5 years old?

These fish have very few years in which to breed.

Fish are currently being killed at such a rate that for some species (e.g. cod and haddock), the numbers that survive until they are old enough to breed may not be sufficient to guarantee the survival of the population. (Remember from Section 6.1 that even though millions of eggs are produced by teleost fish, only a small proportion of them survive to become little fish.)

For a given species, the total weight of sexually mature fish alive in the sea at any one time is known as the *spawning stock biomass* (SSB) (Figure 11.8). When the SSB is low, there is an increased probability that relatively few young fish will be produced. However, environmental factors also play a large part in determining the number of young (e.g. young plaice can be adversely affected by a late spring bloom; Section 9.2). As a result, there may be 'bad' breeding years when the SSB is high, and vice versa. In the case of severely overfished stock, if the few years for which an individual is old enough to breed are environmentally poor ones, that individual will effectively produce no young during its lifetime.

According to Figure 11.8, which North Sea fish species has shown the greatest fluctuations in spawning stock biomass? And which currently has the lowest spawning stock biomass (assume that the trends shown have continued)?

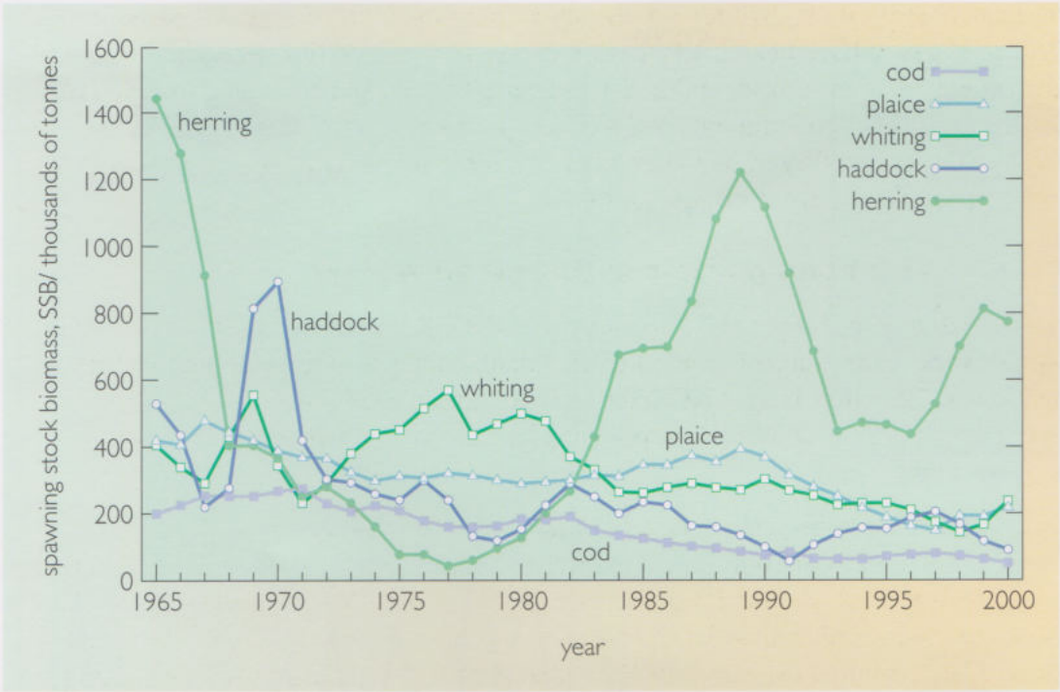


Figure 11.8 Changes in spawning stock biomass (in thousands of tonnes) of herring, haddock, whiting, plaice and cod in the North Sea between 1965 and 2000. *Note* Different species grow at different rates and can attain different maximum sizes; for example, a two-year-old whiting is about 26 cm long, but a four-year-old cod is about 78 cm long.

The herring SSB has shown the most dramatic fluctuations, declining to about 1/30th of its maximum size in the mid- to late 1970s. Currently, the fish with the lowest SSB is cod.

The SSB curve for herring reflects the fact that after a good year in 1965, North Sea herring were virtually wiped out by the mid-1970s, by a combination of overfishing and poor breeding years. Fishing for herring in the North Sea was then prohibited for several years and the stock recovered during the 1980s, probably aided by favourable environmental conditions and the fact that by-catch of herring was reduced in other fisheries that were restricted during that time. By 2004/5, herring stocks were again supporting profitable fisheries.

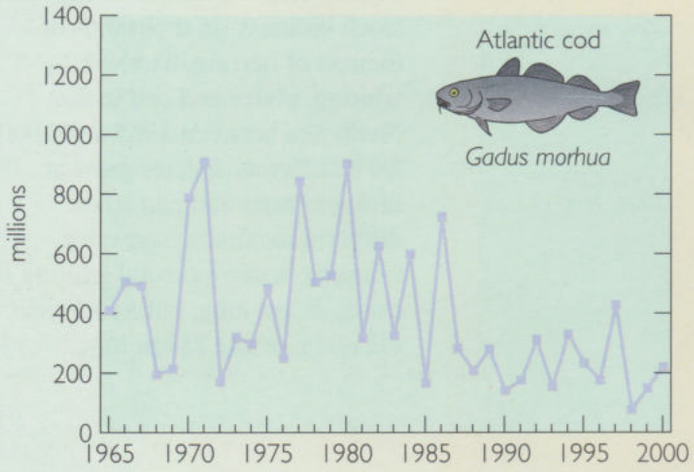
Because such a large proportion of mature fish are killed each year by fishing, many fisheries now largely depend on small, young fish (known as *recruits* because they are joining the stock). Figure 11.9 (overleaf) shows data for numbers of recruits to stocks of cod, plaice, whiting, haddock and herring between 1965 and 2000. Study the plots, and note that the values on the vertical axes for plots (d) and (e) differ significantly from those for (a)–(c).

Question 11.3

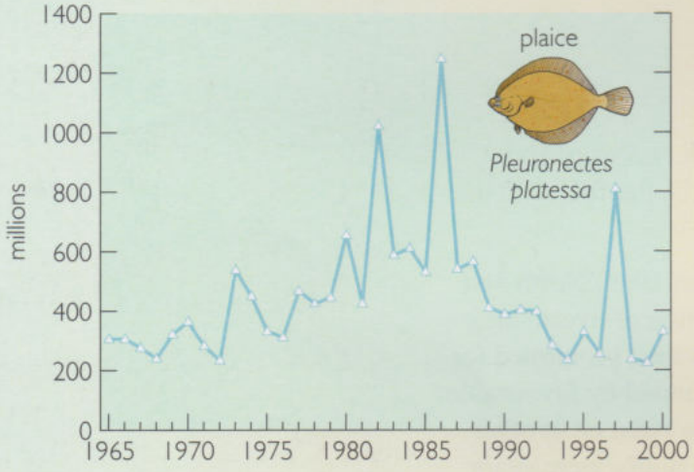
(a) (i) Would you say that any of the plots in Figure 11.9 show any trend or pattern over time?

(ii) Which species of fish shows the greatest *variability* in recruitment from one year to the next over the time period shown?

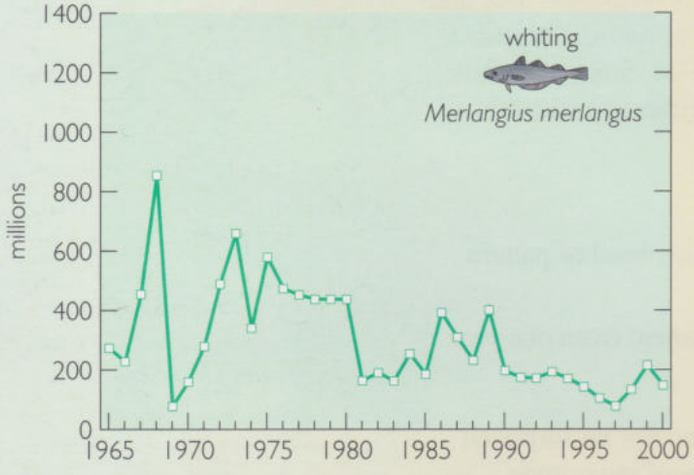
(b) Thinking back to the Blue Planet programmes, why should you not be surprised that numbers of herring shown in Figure 11.9 are about two orders of magnitude greater than those of cod? ◀


Atlantic cod
Gadus morhua
millions
1400
1200
1000
800
600
400
200
0
1965 1970 1975 1980 1985 1990 1995 2000

(a)


plaice
Pleuronectes platessa
millions
1400
1200
1000
800
600
400
200
0
1965 1970 1975 1980 1985 1990 1995 2000

(b)


whiting
Merlangius merlangus
millions
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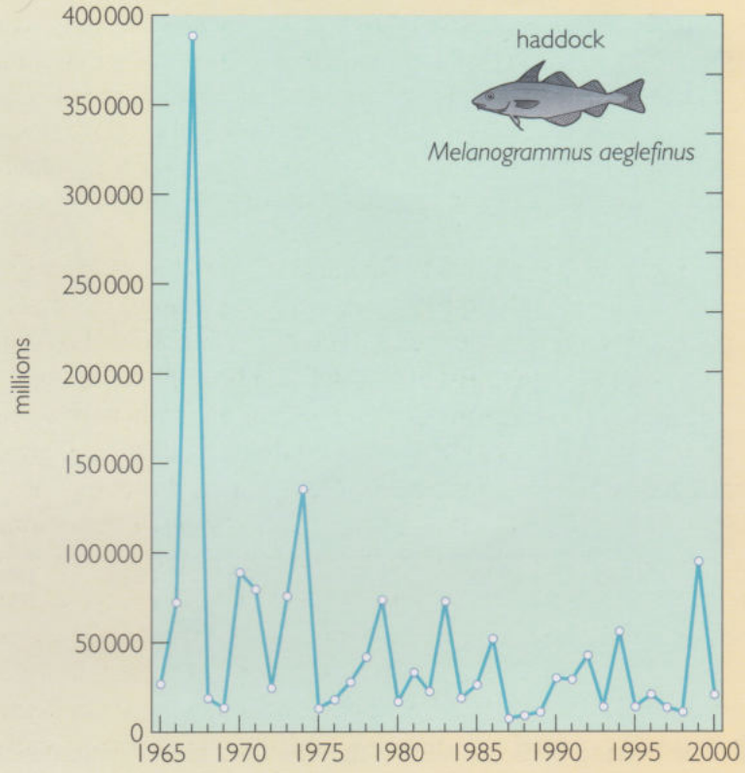
(c)


haddock
Melanogrammus aeglefinus
millions
400000
350000
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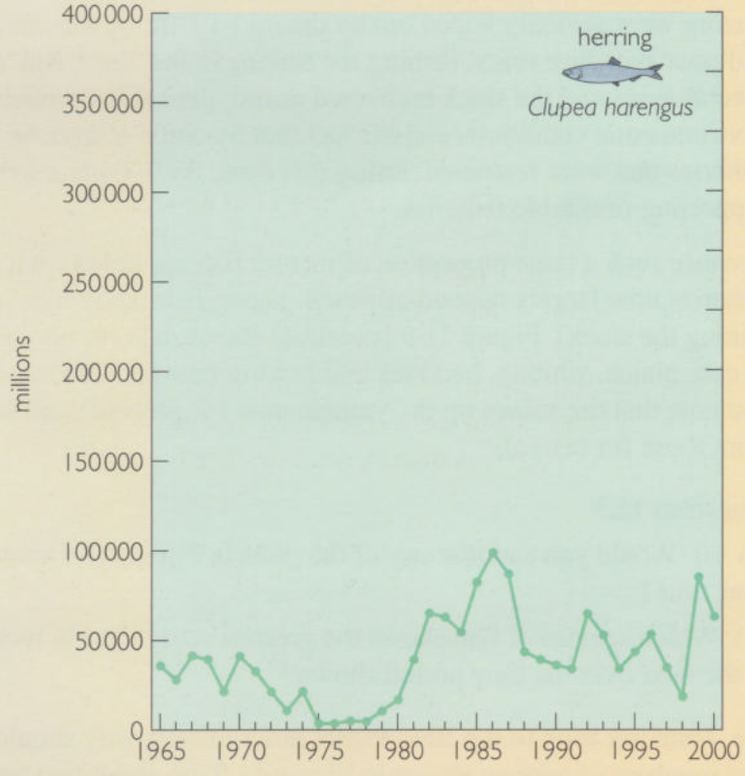
(d)


herring
Clupea harengus
millions
400000
350000
300000
250000
200000
150000
100000
50000
0
1965 1970 1975 1980 1985 1990 1995 2000

(e)

Figure 11.9 (*opposite*) Changes in the number (in millions) of recruits joining the North Sea stocks of cod, plaice, whiting, haddock and herring each year between 1965 and 2000 (the small illustrations are only roughly to scale). Note that values on the axes of (d) and (e) (haddock and herring) are two orders of magnitude greater than those on the axes of (a)–(c) (cod, plaice and whiting). Abundances are for fish in their first or second year of life, but the exact ages of the fish vary from species to species; e.g. the cod data are estimates of the numbers alive in the autumn of the year of their birth (when they have moved to the sea-bed and are in adult form), at which time they are 8–9 months old; whiting, plaice and haddock data are estimates of the numbers alive in the January of their second year, when they are 9–11 months old.

The consequences of marked fluctuations in recruitment may feed through into subsequent years – a good example of this is the effect of the 1904 'year class' (i.e. the fish born in 1904) on the Norwegian herring fishery, which can be seen clearly in Figure 11.10. It may seem surprising that the numbers of young recruits joining the stock each year could have such an enormous influence on the size of the stock. However, as discussed in Section 9.2 in the context of plaice, the first few weeks/months are the most hazardous period of a fish's life, and compared to the losses sustained by the population at this early stage of the life-cycle (particularly in a bad year), causes of natural mortality later in life are relatively insignificant. In other words, it is at the start of the life-cycle that the numbers within a particular year class are determined, and these numbers can vary dramatically between 'good years' and 'bad years'. As older fish are increasingly removed from the population, fisheries are having to depend more on young fish, so fluctuations in recruitment are increasingly reflected in catch sizes.

You may have been wondering how plots like those in Figures 11.9 and 11.10 are compiled. The answer (which you are not expected to remember!) is that numbers are estimated by 'virtual population analysis', which uses the numbers of fish of each age killed by fishing, together with assumptions about natural mortality (for which there is a lack of reliable information), to calculate the numbers of very young fish that must previously have been present. The numbers of fish in recent year classes (for which fisheries data will be incomplete) are estimated from research vessel catch rates together with 'virtual population analysis' estimates from earlier years. As you can imagine, making such estimates is time-consuming and fraught with difficulties.

To some extent, investigating the age structure of populations of fish living in waters like those of the North Sea is simplified because temperature and food supplies show a marked seasonal pattern (Section 4.3). This means that, at least for the first few years of their lives, individual year classes can be identified by how big (i.e. how long) they are.

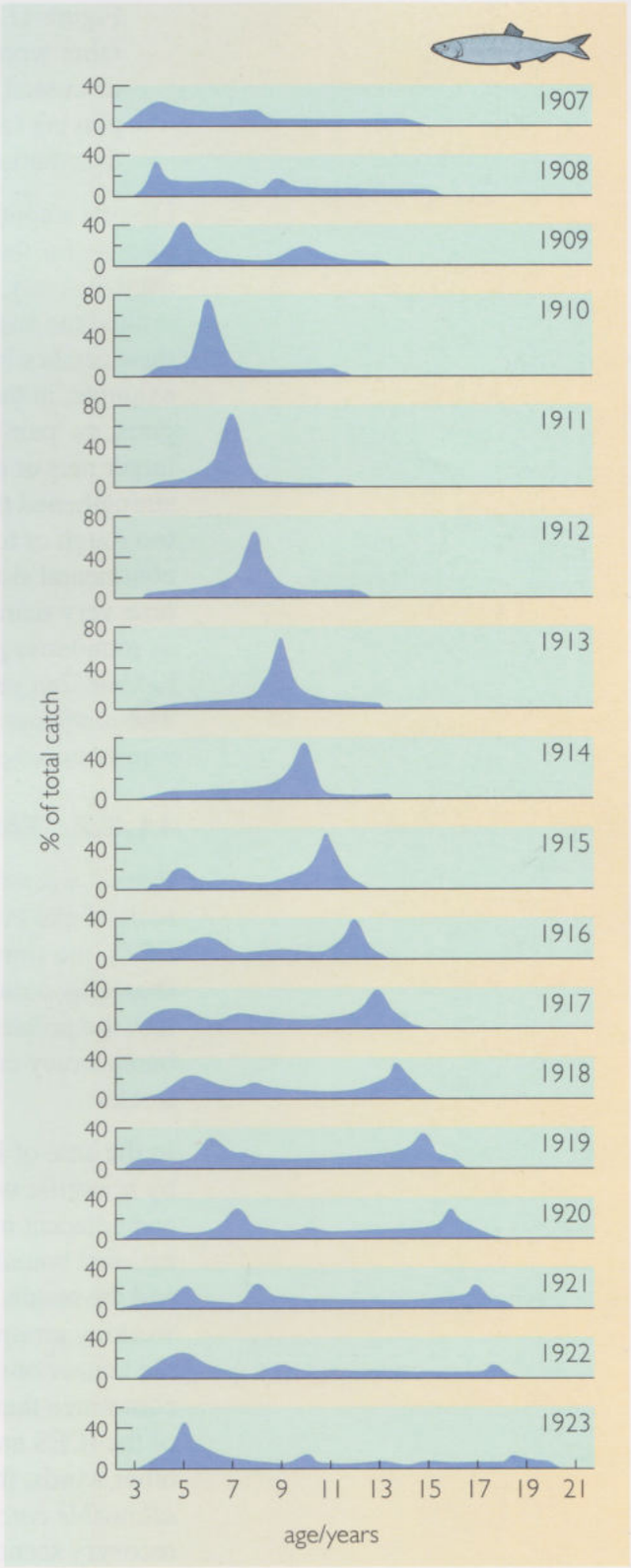


Figure 11.10 Plots to show how herring (*Clupea harengus*) of the 1904 year class, having become large enough to be caught in 1907, then dominated the catch in the Norwegian fishery for a considerable number of years.

- Although it is accepted that environmental conditions affect recruitment, many approaches to fisheries management still assume that, overall, the SSB will be the most important factor determining recruitment, and hence the future size of the stock. Does comparison of the SSB plots in Figure 11.8 with the corresponding plots for recruitment (Figure 11.9) suggest that this is true?
- Even taking into account the time lag between spawning and fish joining the stock, it is very hard to see how the shapes of any of the recruitment plots in Figure 11.9 could have been predicted from the corresponding SSB plot. In other words, SSBs are *not* reliable indicators of future stock sizes. As will be discussed in Section 11.5, climatic fluctuations (and global warming) are playing (and have played) a significant role in determining the sizes and distributions of fish stocks.

Despite a continuing growth of scientific knowledge about fish populations and the reasons for their decline, successive European governments have been unwilling to act decisively, and stocks continue to diminish. Meanwhile, fishermen working around the British Isles (like their counterparts world-wide) attempt to maintain their catches by becoming more 'efficient' and fishing further from home. For example, in the North Sea and the English Channel, many skippers now fish in pairs, as 'pair-trawling' allows them to increase their catching power by towing larger nets or double ('twin') trawls. Other skippers have bought larger vessels and strengthened their gear to enable them to fish on grounds that used to be considered too rough or too deep for trawling. Scottish trawlermen now routinely fish on the continental slope at depths of 500–1000 m to hunt down large monkfish, which are now very scarce on the continental shelf, and to catch non-traditional species such as roundnose grenadier (a type of rat-tail), blue ling, black scabbardfish and black halibut. Ten years ago, these fishermen seldom needed to fish deeper than 250 m. The problems associated with the general trend towards fishing in ever-deeper waters (touched on in 'Deep Trouble', sequence 4) are discussed in Section 11.4.3.

11.3.2 TACs and other management options

Putting scientific advice into practice is easier said than done. For nations such as Iceland and Peru, which have sole jurisdiction over the fishing grounds in their EEZs, the situation is relatively straightforward. However, where resources are shared by a number of nations, as in the case of waters under the jurisdiction of the EU, the problem is more intractable, and conflicting national interests and bureaucracy can conspire to undermine the efforts of those trying to conserve stocks.

In the case of EU waters, the size and health of each fish stock is assessed annually by scientific working groups, whose members come both from EU member states and adjacent non-member states such as Norway (fish pay scant attention to national boundaries). Stock assessments are based on national fisheries statistics and the results of surveys undertaken on research cruises. The findings of the working groups are scrutinised by a committee of eminent scientists working under the banner of the International Council for the Exploration of the Sea (ICES). This committee then sets out a number of management options for each species in each of the ICES areas (there are three such areas in the North Sea, for example). In other words, the committee proposes a number of alternative quotas, or *total allowable catches (TACs)*, each geared (in theory at least) to a particular stock-recovery scenario.

These various management options are sent to the European Commission in Brussels. Here, another scientific committee evaluates the options before presenting them to the EU Council of Ministers. The Council then has the final say on which TACs should be adopted for the next year, taking account not only of the need to conserve fish stocks, but also of broader social and political considerations. For each species, the total TAC is then divided up between the member states and third-party states such as Norway, with each state being allocated a fixed percentage of the TAC, based on historic catches; this is known as the 'principle of relative stability'. (EU vessels with the appropriate licence are allowed to take a specified quantity of fish from Norwegian waters.)

Because each Minister is under pressure from his or her national fishing industry to increase the annual TACs, or to ensure that any reductions are as small as possible, the TACs chosen by the Council of Ministers have tended to be at the upper end of the range of management options on offer, although most fisheries scientists would favour the adoption of smaller TACs, intended to allow the stocks to recover more rapidly. Recently, Ministers have begun to recognise that many stocks are in urgent need of greater conservation and have become more willing to make politically unpopular decisions. Nevertheless, in many cases they are still not taking the decisive action that is needed.

As an example, let's look briefly at the sad case of cod. By 2000, SSBs for cod in the Irish Sea and North Sea had reached their lowest recorded levels (cf. Figure 11.8), and it was feared that these stocks were on the way to becoming effectively extinct as far as fishing is concerned (i.e. 'commercially extinct'). The scientific advice to the EU was that even drastic reductions in TACs would not, on their own, be sufficient to allow these stocks to regenerate. So to protect the spawning fish, fishing for cod was prohibited in the northern part of the Irish Sea for 11 weeks in the spring of 2000. In 2001, similar measures were applied to parts of the North Sea (Figure 11.11) and to the fishing grounds west of Scotland. Despite continued conservation measures, by 2005 the stock was about 53 000 tonnes, which is one-third of the 150 000 tonnes regarded as the bare minimum for survival of this cod population. To prevent cod stocks in the North Sea, Irish Sea and west of Scotland from going the same way as those off north-eastern Canada (see Section 11.3.4), ICES has been calling for a complete ban on cod fishing in those areas. At the time of writing, this advice has so far not been heeded. In December 2005, the EU Fisheries Council cut the number of days a cod trawler is permitted to spend at sea in 2006 by 5%, rather than the 15% cut recommended by the European Commission (or the complete ban recommended by ICES). Furthermore, there were increases in the quotas for other fish stocks for which catches typically include significant by-catch of cod. Many scientists fear that, having failed to grasp the nettle in 2005/6, the EU Fisheries Council have sealed the fate of cod stocks around the British Isles, at least for the foreseeable future.

It is understandable that Fisheries Ministers seek to protect the livelihoods of their state's fishermen, even if their choices of TACs etc. are short-sighted. Furthermore, management systems based primarily on TACs and quotas have the fundamental problem that fishermen can be forced to choose between dumping large catches of marketable fish and making illegal ('black') landings – which many bitterly resent. For most fisheries, in addition to TACs there are also 'technical' regulations stipulating the minimum mesh size that can be used, and the minimum size at which fish can be landed for sale. Unfortunately, these measures bring their own difficulties.

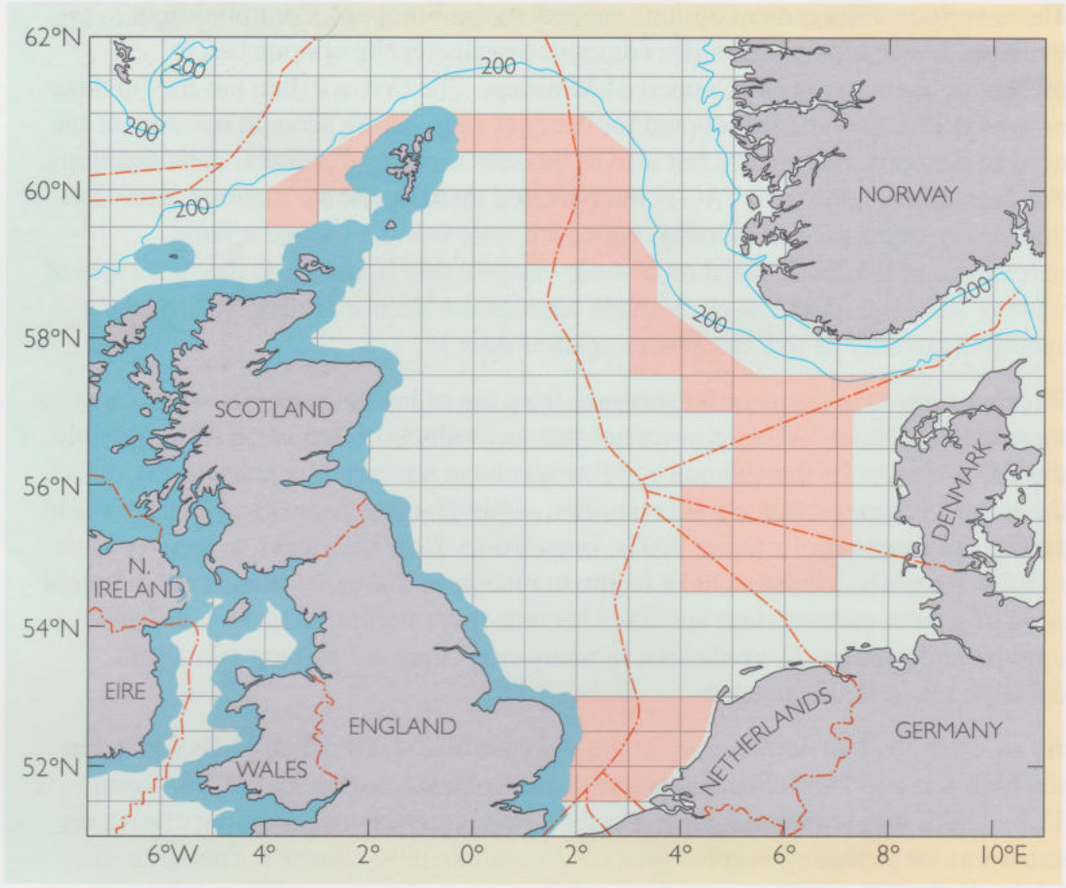


Figure 11.11 Cod fishing grounds in the North Sea closed to fishing for three months in early 2001 (pink areas). The red dashed lines are the boundaries between the EEZs of countries around the North Sea (cf. Section 11.2.3); the blue coastal strip around the British Isles is the UK's 12 n.m. territorial sea (over which it has complete sovereignty). The blue line is the 200 m depth contour.

Can you suggest why selecting an appropriate mesh size is often likely to be problematic in commercial terms?

A given area or volume of sea will support a variety of species of fish, which will be netted together. A mesh size appropriate to the conservation of a large species such as cod would allow almost all the individuals of smaller species that are commercially valuable (e.g. whiting) to escape from the net.

Fisheries that explicitly target more than one species are known as 'mixed fisheries'. The choice of mesh size for use in a mixed fishery is inevitably a compromise.

Another approach is to impose limitations on the amount of resources that are expended on fishing, commonly referred to as *fishing effort* – limiting fishing effort could include restricting the number of days a vessel may spend at sea (as discussed above, in the context of cod), imposing closed seasons and/or closed areas (cf. Figure 11.11), restrictions on the types of fishing gear to be used, and financial constraints. Quantifying fishing effort is not at all straightforward: consider, for example, the practicalities of determining the relative effectiveness of different types of fishing gear being used by different sizes of vessels.

Despite these difficulties, quantifying fishing effort can be useful because it provides information about the state of the stocks being fished: if catches of a particular fish

stock are falling, it could be that the size of the population is declining, or that less effort is being put into catching them; however, if catches are falling (or remaining constant) even though *more* effort is being expended, it can safely be assumed that the population is declining.

11.3.3 The EU Common Fisheries Policy (CFP)

Fish stocks in EU waters are managed under a Common Fisheries Policy (CFP), which came into being in 1983. The CFP deals with conservation of fish stocks, vessels, port facilities and fish-processing plants, and the communal organisation of the market. In addition, it implements an external fisheries policy which includes fishing agreements with non-EU members and negotiations within international organisations. There is a certain amount of incompatibility between the objectives of these activities: on the one hand, the CFP aims to conserve fish stocks, which inevitably means reducing the size of the fishing fleet (and subsidising the decommissioning of fishing vessels); on the other hand, it aims to increase the efficiency of fishing fleets (and subsidises the construction and renovation of fishing vessels).

This incompatibility of objectives stems from the fact that the CFP was originally formulated to deal only with commercial fisheries, but in 1992 the *Treaty of Maastricht* stipulated that environmental protection must be integrated into EU policies, and the CFP's objectives were therefore extended to include protecting and conserving living marine aquatic resources and providing for sustainable exploitation of commercial species.

Under the CFP, decisions on the sizes of annual TACs, together with other measures intended to conserve fish stocks (such as setting minimum mesh sizes and minimum landing sizes, and imposing closed seasons), are made in Brussels. However, member states are responsible for collecting their national fisheries statistics, enforcing catch limits and ensuring compliance with other regulations within their own EEZ. The UK, which has a relatively large EEZ (partly shown in Figure 11.11), employs numerous Fishery Officers to monitor quayside landings, and has several fishery protection vessels which constantly patrol home waters to ensure that British and foreign vessels operating within the UK EEZ comply with the law.

There is also a small EU Inspectorate whose role is to ensure that national enforcement authorities apply the same standards of quality and fairness in their enforcement. New technologies are used to transmit data to the authorities and to monitor the activities of larger vessels through satellite tracking systems. In the Norwegian sector of the North Sea, Norwegian fishery patrol vessels enforce regulations on mesh sizes and discarding of by-catch which are even more stringent than those set by the EU.

One of the more contentious issues surrounding the CFP is the problem of access to 'national' waters. The CFP starts from the premise that EU waters (i.e. the EEZs of states in the EU) are open to all member states. However, there are regulations which exclude new member states from waters in which they have not traditionally fished.

Many fishermen complain that 'their' fish are being exploited by so-called quota-hoppers (also known as 'flagships'). These are fishing vessels that are registered in one state, and have an entitlement to take a share of that state's quota of fish, but have been bought by an individual or registered company of another state. Thus, it is not uncommon to see (for example) UK-registered fishing vessels, often crewed by non-

UK nationals, operating out of ports in continental Europe. Such vessels are operating perfectly legally.

Another cause for complaint are reports of large Eastern European factory trawlers 'hoovering up' fish in UK waters. In fact, these vessels were prohibited from fishing in EU waters many years ago. Factory trawlers are often seen in British ports, or anchored in inshore waters, but they are there only to buy and process herring and mackerel caught by UK-based fishermen.

Drift nets, the Mediterranean and the CFP

An example of how ineffective the CFP has been in its efforts to conserve fish stocks is provided by the issue of drift nets. It has long been acknowledged that drift nets are environmentally harmful (Section 11.2.2), but the EU took six years to accept the UN resolutions (made in 1989 and 1991) to prohibit the use of drift nets in international waters from 1992, and took 10 years to make the ruling legally binding.

One of the problems of the CFP is that in many respects, including those relating to conservation, it has from the beginning been tailored to the north-east Atlantic and adjacent waters. The drift-netting issue came to the fore as a result of negotiations in connection with the 'Mediterranean regulation', an attempt to design a set of rules to suit the specific circumstances of the Mediterranean. As a concession to Mediterranean fishermen, it was proposed that 'anchored drift nets' (Figure 11.5), which are favoured in the Mediterranean, would be exempted from the drift-net ban. This inconsistent approach provoked vociferous objections from conservation groups, who feared it would threaten the progress already made in the banning of drift nets, including a recent drift-net ban in the Baltic.

In any case, drift-netting is still in widespread use in the Mediterranean (as elsewhere), and is a common component of EU fleets. In the Mediterranean and adjacent waters, there are currently about 500 drift-net boats, 60% of which belong to EU member countries (notably France and Italy), or prospective members (Turkey and Morocco). Much of this drift-netting is illegal, but in some cases it has been made legal by renaming the fishing gear: Italy allows the use of the *ferrattare*, which resembles a drift net, and a French national decree adopted in 2003 authorised the use of the *thonaille*, a drifting gill net for catching tuna (although, following intervention by conservation agencies, this was declared illegal by a French court in August 2005).

In order to decommission the drift-netting fleets, the EU offered financial compensation where vessels were fishing illegally. However, despite enormous subsidies to ship-owners and fishermen, illegal drift-netting continued, and is continuing. Governments of Mediterraean countries belonging to the EU have not only failed to police the law effectively, but have also tried to find ways around it and have colluded with illegal drift-netters. Furthermore, boats that *have* been decommissioned have been sold for use by countries like Morocco and Tunisia, which as yet are not part of the EU.

This story demonstrates three of the CFP's most pressing challenges: designing policies that are workable in a wide range of fisheries and environmental circumstances; effectively policing regulations aimed at conservation of stocks, given lack of resources and the possibilities for corruption; and managing subsidies in such a way that they result in real rather than illusory decreases in fishing effort.

A reformed CFP

The CFP was reformed in 2002, and is continuing to bring in new regulations associated with the reform. Here is a brief summary of the main changes.

The CFP's explicit commitment to conservation and sustainability is much stronger than previously. Significantly, the precautionary principle is built into its objectives; this means (in theory, at least) that where there is a threat of serious or irreversible damage to fish stocks or the marine environment, a lack of definite scientific evidence should not be used as a reason for postponing conservation measures. You may like to consider whether recent (2005) decisions by the EU Fisheries Council regarding limits on fishing for cod (Section 11.3.2) were consistent with the precautionary principle.

It is now accepted that the CFP should integrate wider environmental issues into policy-making, and move progressively away from a stock-by-stock approach, towards ecosystem-oriented management. This approach is necessary not only because vulnerable species and habitats are adversely affected by fishing, but also because commercially exploited fish stocks are themselves integral and extremely important components of the marine ecosystem. If the ecosystem management approach is to be successful, the quality of scientific advice provided to the EU must be improved; it will be necessary to learn more about the biology of exploited and unexploited species, and to improve our understanding of how ecosystems function and how they are likely to react to different types of fishing pressure and exploitation strategies. (In Section 11.3.4, you will see just one example of what can happen to an ecosystem when fish stocks are overexploited.)

There has been an improvement in the way subsidies are to be handled. In the past, subsidies for decommissioning fishing boats could be used in such a way that the overall result was not a decrease in fishing! No longer can funds intended as compensation for refraining from fishing be legally used to fund the building of new boats; neither should it be possible legally to sell on decommissioned boats or gear (as occurred in the Mediterranean in the context of drift-netting) – this practice is referred to as 'exporting fishing capacity'. How well these new measures work will depend on how well they are policed, and the political will of the individual governments concerned.

Before the reforms, the fishing industry had taken no part in the setting of EU TACs (apart from lobbying Ministers). Renegotiation of the CFP provides opportunities for major stakeholders in the marine environment – fishermen's organisations, fish processors and environmental organisations – to play a more active part in management of fish stocks. This should be beneficial because fishermen are more likely to be convinced by the assessments if they have contributed to them. It seems likely that a revised CFP will allow for more management decisions to be taken at a local level, allowing rapid responses to local circumstances and emergency situations.

The scandal of EU Third Party Fishing Agreements

Because many fish stocks in EU waters have been seriously overfished, European fishing vessels are now working in the EEZs of other countries (typically developing countries), through negotiation of Third Party Fishing Agreements. As the countries involved generally have no large fishing fleets of their own, they hope to benefit from the living marine resources in their EEZs through fees paid by other countries. However, despite the reformed CFP's conservation-oriented policies, EU fisheries

agreements are resulting in unsustainable practices in the waters of non-EU countries, and are creating socio-economic problems for those countries.

One of the areas targeted by EU fishing vessels is the highly productive upwelling area off west Africa (cf. Figure 11.2 and Question 11.1b). In 2002, the EU paid Mauritania £300 million for the rights to fish for five years in its EEZ. One of the vessels to be found working these waters is the 14 000-tonne *Atlantic Dawn*, the largest fishing vessel ever built, whose purse-seine net has been described as having 'twice the volume of the Millennium dome'. The *Atlantic Dawn* was built in Norway for Ireland; although the European Commission considered that the Irish fishing fleet was already too large at the time (2000), it sanctioned the addition of the super-trawler, as long as it never fished in EU waters.

11.3.4 What happens when fisheries management fails: the collapse of Canadian cod stocks

Commercial extinction of cod has already happened off the eastern coast of Canada. Here, several economically important cod stocks, including those on the Grand Banks off Newfoundland, first collapsed in the early 1970s. A quota system was introduced in 1974, but subsequent policy decisions based on incorrect scientific estimates of the size of cod populations meant that there was a second and more enduring collapse in the early 1990s. It turned out that official estimates of cod deaths by fishing had been too low – information obtained through surveying and tagging later showed that overcapacity in the fishing fleet had resulted in increased discarding of juvenile fish in favour of large fish – perhaps one-third of juveniles were being caught and discarded (i.e. killed).

In 1992–93, the Canadian Government imposed a moratorium on commercial fishing for cod to allow the stocks to recover, although it was known that this decision would create considerable social and economic hardship for local communities (many of which were almost entirely dependent on fishing), not to mention political problems for those who introduced the moratorium. Fisheries scientists predicted that a fishing moratorium of two to four years would be sufficient to allow the cod stocks to recover. When there were signs of possible recovery, some fisheries were partly re-opened, and the small increase in stock size was quickly wiped out. More than a decade later there is still no significant recovery.

Interestingly, when cod catches plummeted in 1991, the value of the catch per tonne shot up from Can$600 to about $1300, and from 1997 onwards the value of the catch was consistently higher than the value of the catch in 1972 when catches were ten times higher. This strongly suggests that regulating exploitation of fish stocks by using market forces does not work.

As the Canadian cod stocks have continued to struggle, there have been calls for increased culling of seal populations, particularly harp seals (*Phoca groenlandica*). Many fishermen believe that harp seals consume significant quantities of cod. However, harp seals have a broad diet of about 50 species of fish and invertebrates (some of which themselves eat cod), and there is now a growing consensus that predation by harp seals is unlikely to be a major factor in preventing the recovery of cod stocks.

Many marine biologists now think that the reason that Canadian cod populations have not recovered is that most of their larvae are dying of starvation.

Thinking back to the cod life-cycle shown in Figure 11.3, can you remember what larval cod feed on?

Larval cod feed on zooplankton.

Larval cod prefer copepods, particularly the species *Calanus finmarchicus*, shown in Figure 1.10c. In a 'good year', newly hatched cod larvae will find abundant supplies of the early larval stages of *Calanus finmarchicus* (these look rather like the early barnacle larva shown in Figure 4.12g). The cod larvae will prosper and become juvenile cod, and after six weeks those juveniles that have survived predation will be migrating down to deeper water (cf. Figure 11.3).

Calanus itself has a complex life-cycle in which late larval stages and sexually mature adults overwinter in deep water (1000–2000 m) in a kind of hibernation. In the spring, they migrate to the surface, moult and spawn. It is thought that, until relatively recently, they were rising to spawn in the vicinity of the cod spawning grounds, but – unfortunately for the cod – changes in patterns of deep-water circulation have meant that the overwintering *Calanus* have been carried way beyond the cod spawning grounds. As a result, the *Calanus* spawning has been of no benefit to the newly hatched cod, and they have starved to death.

As you may remember from Section 11.1, adult cod are demersal, and typically feed on smaller fish, invertebrates, and sometimes animal remains, on or near the sea-bed. As cod stocks fell, the sea-bed ecosystem began to change.

As cod numbers declined, what kinds of animals could have been taking their place in the food web?

The niche was filled by sea-bed carnivores and scavengers, such as crabs, shrimps and lobsters.

As a result of this change, fishing in the area now concentrates on large crustaceans – you may well have seen Canadian lobsters for sale.

The increase in the populations of large crustaceans (and other invertebrates) is not the only change that has been observed. As the cod declined, surveys by the Canadian Government's Department of Fisheries and Oceans (DFO) indicated a several-hundred-fold increase in populations of some small pelagic fishes, including herring, capelin, sand-lance and mackerel.

Can you suggest why there might have been an increase in populations of small fish?

Cod feed on smaller fish, and their populations could have increased as a result of the reduced predation pressure from cod – especially as they grow faster than large fish like cod, and mature earlier.

It may have struck you that the increase in the populations of small fish could help to explain the increase in the number of harp seals; although they prefer large fish, they will also eat smaller fish like capelin and herring.

Things are not that simple, however. Normally, capelin form an important part of a cod's diet, and some biologists had previously linked the decline in cod to a reduction in capelin populations and/or changes in their distribution. Furthermore, the DFO's survey methods have been strongly challenged, and it seems highly likely that the small fish have not increased their populations but simply moved onshore, and changed their depth distribution in the water column, in response to climatically driven changes in the distribution of the various species of zooplankton on which they feed.

There are now no big cod at all in this area, as fish that once lived for 50 years or more (longer than North Sea cod) now die before they are seven to eight years old. By the mid-1990s, some of the medium-sized adult cod being caught over the Canadian continental shelf were very thin. By 2002, some catches contained cod with sunken (often empty) stomachs, arched backs and downturned heads; their mouths were reddened, suggesting excessive foraging on the sea-bed (Figure 11.12). These fish were obviously starving, and their changed appearance suggested that in the absence of their deep-living prey fish, they were driven to live entirely by bottom-feeding.

Figure 11.12 An example of a starved Atlantic cod (*Gadus morhua*), caught off Nova Scotia in 2002. Note its downturned head and reddened mouth. (Tape measure shows the cod to be 1 ft. 7 in. long.)

Furthermore, a long-term study of demersal fish living on the continental shelf off Nova Scotia has shown that over the last four decades, for the resident fish community as a whole (including many species not directly affected by fishing), there have been widespread reductions in body size, reductions in the biomass of the populations, and decline in physiological condition (i.e. the fish are less fit than previously).

There is a school of thought that centuries of fishing have resulted in the permanent removal of biomass from the waters off eastern Canada (cf. Figure 11.2), and has affected ecosystems in a way that has resulted in a decrease in the amount of organic material falling from the surface waters to the sea-floor. However, it is not clear exactly how this could come about: one suggestion is that the increased populations of herring (which, as you know from sequence 11 of 'Seasonal Seas', are plankton feeders) have effectively been intercepting organic material on its way to the sea-floor. Another view is that the permanent removal of biomass by fishing has actually decreased the amount of primary production, as well as production at higher trophic levels – a crude analogy would be the removal of rainforest trees and plants, and the dependent animals, to leave only grassland. We will come back to this idea in Section 11.4.2.

Whatever the full reason, it has been a shock to marine scientists that human activities could bring about such dramatic changes in marine ecosystems; politicians and fisheries managers wanting confirmation that they need to base management decisions on consideration of whole ecosystems rather than the states of individual stocks, need look no further than the sad state of affairs off eastern Canada.

11.3.5 Illegal, unreported and unregulated fishing

As you have seen, laws and regulations relating to fisheries are not always enforced with enthusiasm. Furthermore, many fishing vessels operate illegally as a matter of course, especially if the fish concerned are high-value, and there are those who are happy to buy them, even in the knowledge that the law has been broken. The term illegal, unreported and unregulated (or IUU) fishing covers: (1) all illegal fishing (e.g. a vessel of one state fishing in the EEZ of another without permission); (2) all fishing that takes no account of responsibilities to conserve living marine resources under international law; and (3) unreported (or misreported) fishing, which could be either illegal or unregulated. IUU fishing is a ubiquitous feature of global fisheries; it

occurs in territorial seas, in EEZs and on the high seas, and is practised by small-scale fisheries, factory trawlers and industrial trawlers.

IUU fishing is a problem in itself, because it is often associated with irresponsible and unsustainable fishing practice.

- Can you suggest another reason why IUU fishing is a threat to the conservation of fish stocks?

- It makes determining suitable conservation measures, and hence effective management of stocks, very difficult: if we don't know how many fish are being taken from a population, we cannot make accurate assessments of the health of the stock.

One way of reducing IUU fishing would be to tackle the problem of vessels operating under 'flags of convenience'. The responsibility of documenting a catch belongs not to the state where the catch is landed, but to the state under whose flag a vessel is sailing. Some countries are willing to register fishing vessels of other nations while taking no responsibility for the activities of those vessels.

In recent years, there has been a lot of media attention on illegal fishing of the Patagonian toothfish (*Dissostichus eleginoides*), also known as the Chilean or Antarctic sea bass, which lives in deep waters over seamounts and continental shelves around Antarctica (Figure 11.13). This fish was only discovered about 25 years ago, but is already facing extinction through overfishing. Its high value in countries like Japan and the USA (amongst others) means that some skippers are willing to risk confiscation of an illegal catch and their vessel, along with fines and/or imprisonment, especially as the chance of being apprehended is small. The body responsible for protecting the toothfish – the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) – has introduced a number of measures to address the problem of IUU fishing, including an automated satellite-linked vessel monitoring system, blacklisting of vessels known to be engaged in IUU fishing, and a catch documentation scheme to monitor international trade in the fish.

Figure 11.13 The Patagonian toothfish (*Dissostichus eleginoides*) – a *cause celèbre* in the context of IUU fishing. The toothfish plays an important part in the Southern Ocean ecosystem around Antarctica; it lives on squid and shrimps, and is itself prey for sperm whales and elephant seals. It grows slowly and can attain lengths of more than 2 m. It can live as long as 50 years and does not breed until it is at least 10 years old.

Almost by definition, the extent of IUU fishing is not known with any accuracy (cf. Figure 11.6). However, the Food and Agriculture Organisation (FAO) of the United Nations believes that in some important fisheries it accounts for as much as 30% of total catches – i.e. whatever the reported catch is, the actual catch could be half as much again. In the case of the Patagonian toothfish, IUU fishing probably accounts for half the total catch.

11.4 The legacy of overfishing

In this section, we will look at some of the serious negative side-effects of overfishing. Some are relatively obvious, when we take the trouble to examine the evidence; others are more insidious.

11.4.1 'Fishing down the food web'

Although the amount of effort expended on fishing has continued to increase, the global marine catch has reached a plateau (Figures 11.1 and 11.6) and most ocean fisheries are regarded as 'fully fished' or 'overfished'. In particular, stocks of large

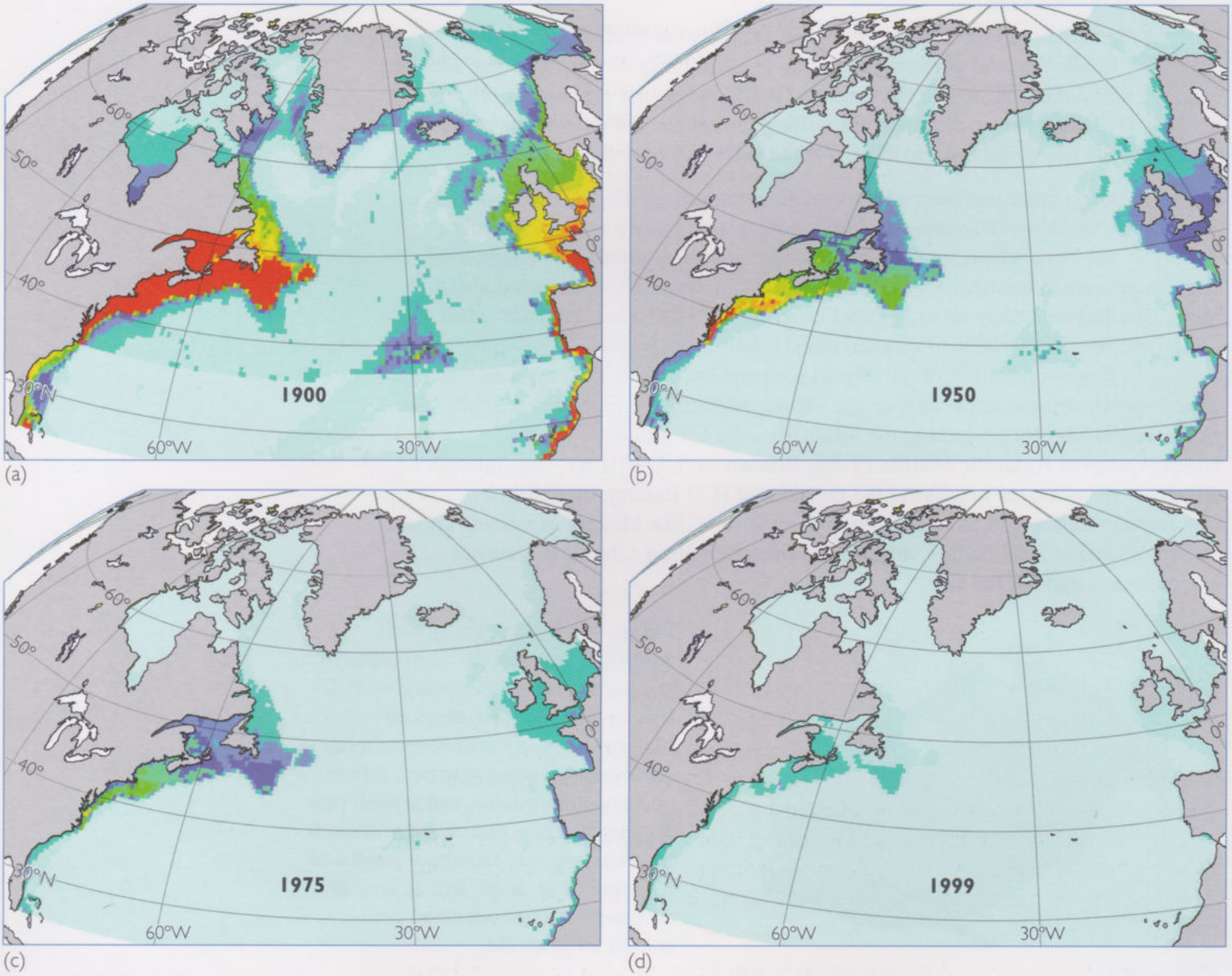


Figure 11.14 Maps showing the decline of large predatory fish in the North Atlantic since 1900, expressed in terms of biomass in tonnes km^{-2} ('large' here means fish at trophic level 3.75 or higher; see text).

carnivorous fish have been plummeting (Figure 11.14). In Section 11.3.4, we discussed the fairly well-known example of the crash in cod stocks off eastern Canada, but it is not just demersal fish like cod which are in severe decline; large pelagic carnivores – fast ocean predators such as tuna (especially bluefin tuna) and marlin – are also becoming increasingly rare.

According to Figure 11.14, where has the decline in predatory fish populations been greatest?

The decline has been greatest over the continental shelves off north-eastern America (the Grand Banks etc.) and over the continental shelf of north-western Europe (the North Sea etc.).

In other words, the decline in predatory fish (in absolute biomass) has been greatest in those areas where they were previously most abundant. In fact, studies of the sizes of catches in a wide range of exploited areas, both open ocean and shelf seas, has shown that in terms of relative decline of abundance, patterns of depletion are very similar worldwide. Consistently, it has been found that within 15 years of modern commercial fishing moving into an area, the abundance of large predatory fish has fallen by about 80% (Figure 11.15).

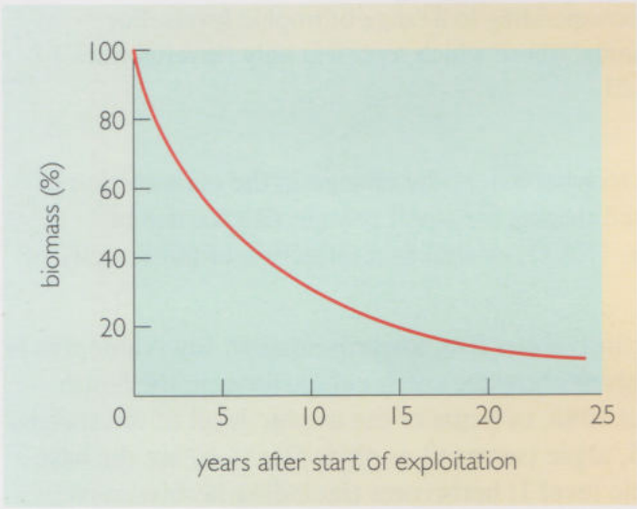


Figure 11.15 The typical pattern of decline of large predatory fish populations, after the introduction of modern commercial fishing (based on data collected by research surveys, and catches by the Japanese long-lining fleet). After 15 years of commercial fishing, only about 20% of the original biomass of large predatory fish remains.

Meanwhile, the composition of catches has been gradually changing as the fishing industry adapted to declining populations, and changed its target species accordingly. Some of the changes have been associated with 'serial depletion' of stocks. This occurs when stocks of a fish in a given area become so depleted that it becomes financially worthwhile for the fishing industry to move onto more distant fishing grounds (using more fuel), or onto another, perhaps smaller, species which previously had not been targeted; when this fishery in turn becomes exhausted, the fishing vessels move on to yet another stock or species.

More generally, there has also been a shift in catch composition away from large, high-value carnivorous fish, towards smaller, low-value fish, which feed at lower trophic levels.

Suggest some examples of small, low-value fish.

Typical examples would be herring, anchovy, sardines and other pelagic shoaling fish (i.e. those referred to as 'bait' fish in the Blue Planet programmes).

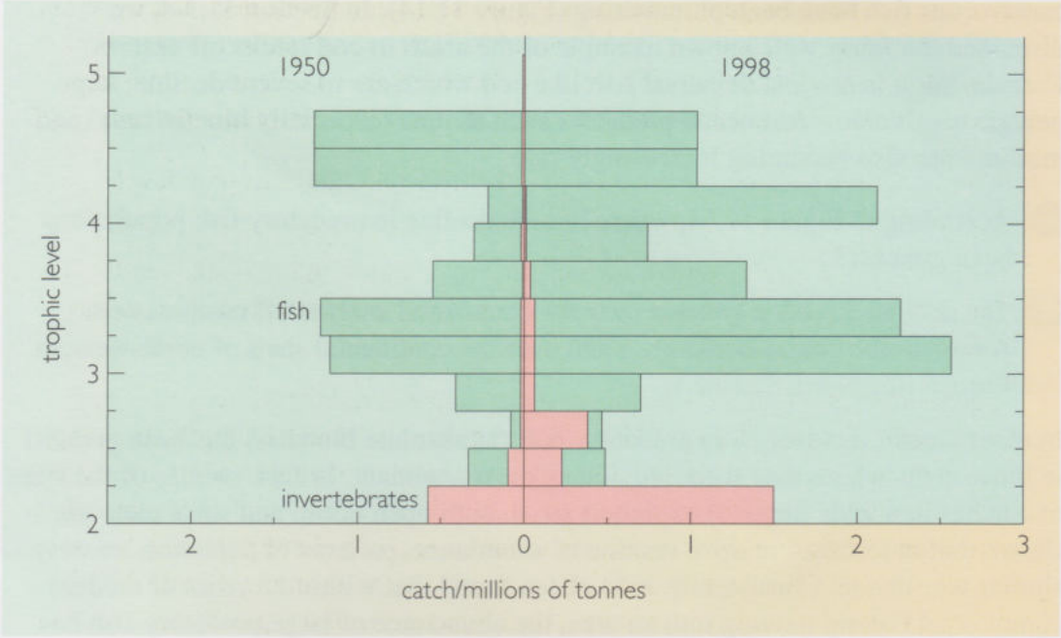


Figure 11.16 How the annual catches in the North Atlantic in 1950 and 1998 broke down in terms of trophic level. The diagram is effectively two histograms turned on their sides, with pairs of columns (bars) corresponding to a range of trophic levels. For example, the lowermost pair of 'columns' (those which represent only 'invertebrates') include species at trophic levels 2–2.25.

It should be said that it is not clear to what extent the change in the composition of catches is a response to the increased market for small pelagic fish for use in fishmeal (as you will see in Section 11.6.1), as well as a reflection of the scarcity of larger fish.

This trend from large, high-value carnivorous fish, towards smaller, low-value fish is illustrated by Figure 11.16, which shows how the catch composition in the North Atlantic changed between 1950 and 1998, in terms of the trophic level of the species caught. As discussed in Section 5.5, algae (seaweed or phytoplankton) are the base of the food web and so are at trophic level 1; herbivores (including herbivorous zooplankton) are at trophic level 2; carnivores (including carnivorous zooplankton) that feed on herbivores are at trophic level 3; and carnivores that feed on smaller carnivores are at level 4 or higher (depending on the trophic level of their prey species). In reality, most marine animals have mixed diets – e.g. as well as feeding on diatoms, krill may consume herbivorous zooplankton such as copepods, and so can be at level 2 or level 3. Similarly, a shark feeding on cod that are at trophic level 4 will itself be at trophic level 5, but if half the shark's food consists of smaller fish at level 3, its trophic level will be 4.5.

- According to Figure 11.16, what change was there in the annual catch of animals in the two highest categories of trophic level (4.25–4.5, and 4.5–4.75) between 1950 and 1998?

- On the 1950 side of the diagram, the length of the top two bars corresponds to about 1.3 million tonnes; on the 1998 side, the length of the top two bars corresponds to about 1.0 million tonnes. In each category therefore, the annual catch fell from about 1.3 to 1.0 million tonnes, i.e. by 0.3 million tonnes, giving a total fall (for trophic levels of 4.25 upwards) of $2 \times 0.3 = 0.6$ million tonnes.

In other words, the tonnage of catch at the highest trophic levels declined by about 25% ((0.3/1.3) × 100%) between 1950 and 1998. The overall shift to lower trophic levels is very marked, and one of the most notable features is the increase in the tonnage of low trophic-level invertebrates caught annually between 1950 and 1998.

- What species would be included among the invertebrates at trophic level 2–2.5?
- Typical species would be bivalve molluscs (e.g. clams and mussels), and some crustaceans. Squid are also invertebrates (molluscs) but are predators, so are at level 3 or higher.

Only relatively recently has it become properly appreciated that if *we* are having more and more difficulty locating fish, then large carnivorous fish, and fish-eating marine mammals such as seals and dolphins, will also be having to adapt their diet to what is available. As the seas have become increasingly depleted of fish, particularly the larger specimens of each species, so marine food chains have generally become shorter (i.e. food webs have become less complex). As an example, Figure 11.17 shows how, formerly, large saithe in the North Atlantic would typically feed on cod, which in turn fed on fish like whiting, which consumed haddock, which ate zooplankton, which live on phytoplankton. Now, with cod, whiting and haddock

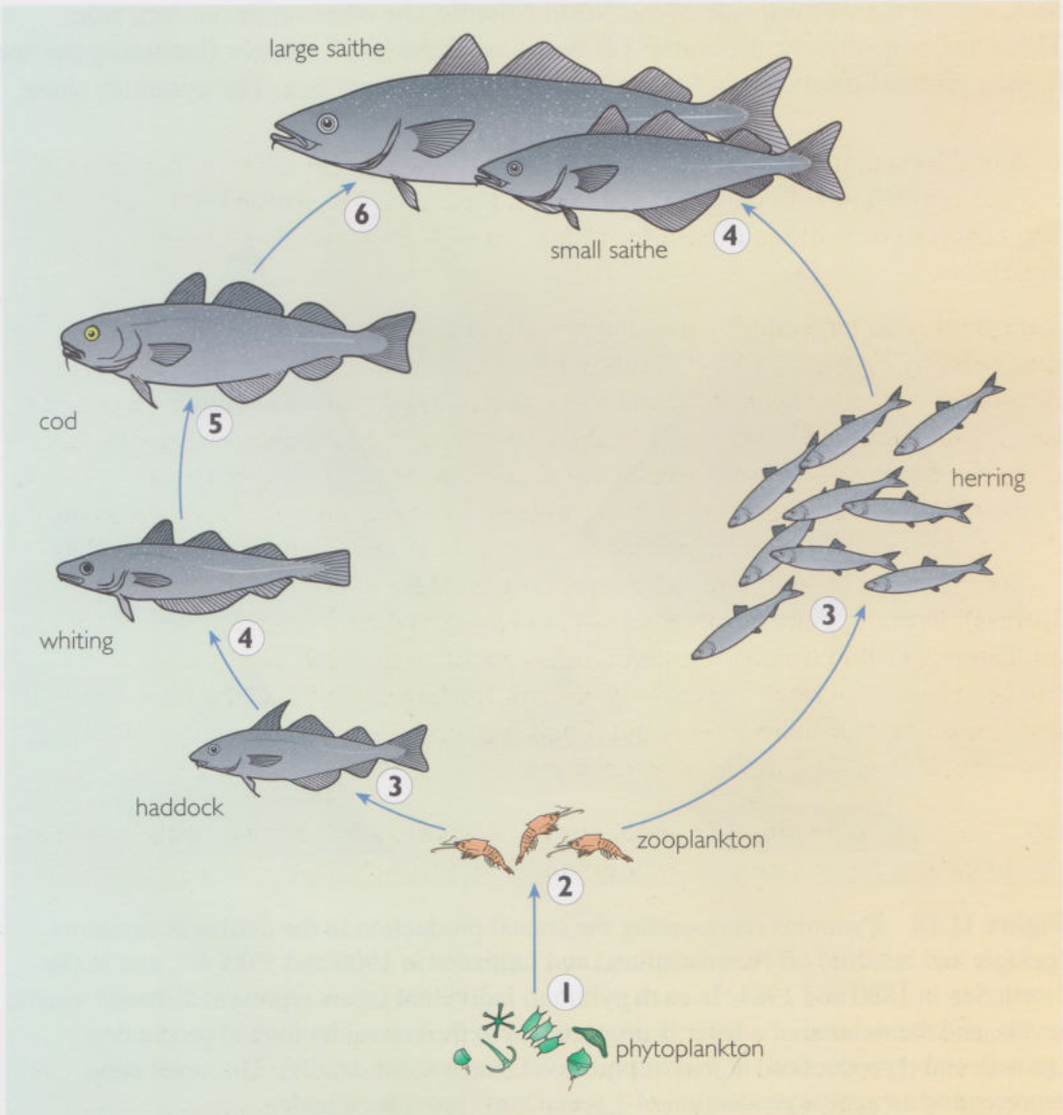


Figure 11.17 An example of the effect of overfishing on the structure of marine ecosystems. Previously, in the North Atlantic, large saithe would be at the top of a food web/chain with six trophic levels (left-hand side). Now, saithe are likely to be at the top of a food web/chain with only four trophic levels, and are themselves likely to be smaller (right-hand side).

becoming scarcer, saithe – which are generally smaller than previously – are more likely to eat small shoaling species ('bait fish') such as herring, which live on zooplankton.

Figure 11.17 is an oversimplification because, as mentioned above, most marine species have mixed diets, and even when the North Atlantic was not overexploited saithe may have taken herring and other fish if cod were less abundant than normal. Furthermore, fish commonly move up the trophic levels as they grow: the larval stages eat plankton, young fish typically eat small invertebrates, and then finally move on to smaller fish (sometimes of their own species). However, adult fish of similar lengths but different species do not necessarily feed at the same trophic level, as their physiology and body design are related to what they eat. For example, in relation to their size, herring have rather small mouths, suitable for taking zooplankton (cf. 'Seasonal Seas', sequence 11), whereas saithe and cod have relatively large mouths, suited for feeding on fish and other fairly large prey.

By being part of a variety of food chains, both short and long, marine predators have a buffer against times when environmental conditions do not favour their preferred prey. Now, for most predatory fish, there is no such buffer to help them through hard times.

Figure 11.18, which is taken from *A Perfect Ocean*, is the result of a detailed analysis of an enormous amount of data relating to the marine ecosystems in two areas of shelf seas, one on the western side of the North Atlantic, the other on the eastern side. These are, respectively, the waters off Newfoundland and Labrador (including the cod fishing grounds discussed in Section 11.3.4) and the North Sea. The pyramids show,

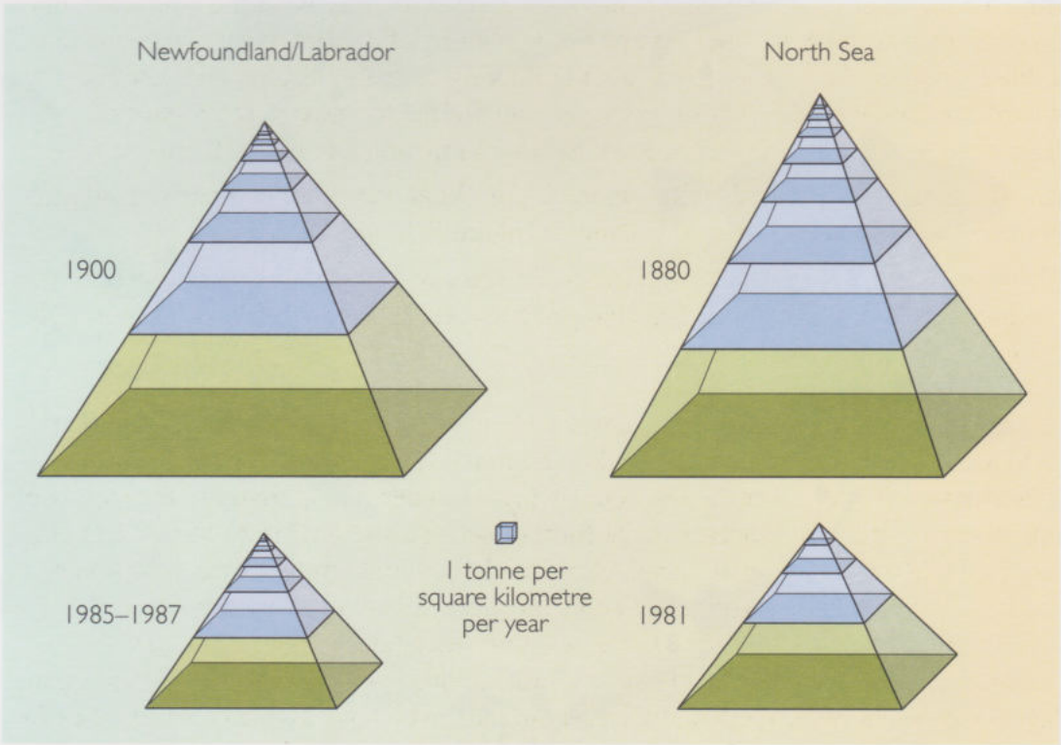


Figure 11.18 Pyramids representing the annual production in the marine ecosystems (pelagic and benthic) off Newfoundland and Labrador in 1900 and 1985–87, and in the North Sea in 1880 and 1981. In each pyramid, individual layers represent different trophic levels, and the volume of a layer is proportional to the annual biological production (growth and reproduction) at that trophic level (see text for details). The small cube representing an annual production of 1 tonne km^{-2} provides a scale.

in graphic form, the effect of overfishing on the number of trophic levels, and the biological production per unit area of sea, in the two areas. The upper pyramids represent the situation in 1880 and 1900, just before the introduction of steam fishing vessels (at a time when there were more than 20 000 sail-powered fishing vessels working in the North Sea). The lower pyramids show the situation about a century later.

In each pyramid, the number of layers corresponds to the number of trophic levels, and the volumes of the individual layers represent the annual biological production at the various trophic levels. Because the pyramids represent the *entire* ecosystems in the areas concerned, they include production (growth and reproduction) by communities in the water column *and* communities on, near and in the sea-bed. The food webs under consideration are extraordinarily complicated, but to some extent they resemble the two linked food chains in Figure 5.11b. To take account of both pelagic and benthic organisms, the lowest layer of each pyramid includes not only photosynthesising primary producers (phytoplankton and seaweed) but also organic detritus and bacteria (consumed by many benthic animals; Sections 3.3 and 10.3), as well as dissolved organic material. The next layer up includes herbivores and detritus feeders; the next, carnivores that feed on these, and so on. The topmost layer represents top predators (mammals, birds and large fish).

Study Figure 11.18 and then answer Question 11.4.

Question 11.4

(a) Has the change in the number of trophic levels been the same in the two areas?

(b) Thinking back to Section 5.5, can you suggest roughly what the volume of the second layer must be, as a percentage of the volume of the first layer? (Assume the value is the same in all four pyramids.) Following on from this, explain whether you would expect the volumes of higher layers, and of the topmost pyramid-shaped 'layer', to be the *same* percentages of the layers immediately below them?

(c) Compare the pyramids with Figure 5.11b. What does your comparison suggest about the data on which the food chains in Figure 5.11 were based?

(d) According to Figure 11.18, how would you say the total annual production of biomass per km^2 of the North Sea changed between 1881 and 1981? (Make a rough estimate only.) ◀

You may well have wondered why Figure 11.18 seems to show that annual primary production off Newfoundland/Labrador and in the North Sea has declined since 1880/1900. After all, over the last century there has been an *increase* in the supply of nutrients to continental shelves in the form of sewage and fertilisers carried from the land, so a decrease in primary production would be highly unlikely (and there is no evidence for it). The answer to this apparent paradox is that the pyramids were effectively constructed from the top down, with each layer representing the production needed to support the layer above. In other words, the sizes of the upper layers (representing production by larger animals, which is easier to quantify) has to a large extent determined the sizes of the lower layers.

If we accept that annual primary production has *not* decreased in the two areas (and that the research on which the pyramids are based is sound), we are left with two possible scenarios that could explain a reduction in the amount of primary production and detritus consumed by the animals represented by the next layer up. The first scenario – for which there is no evidence – is that a large amount of

uneaten plant debris, and other detritus, has been accumulating on the sea-bed off Canada and in the North Sea.

Can you suggest what the other scenario might be? (*Hint:* Think back to Question 8.4b, about why the Arctic food web shown in Figure 8.4 is incomplete.)

It is possible that the 'extra' primary production and detritus is being consumed by a group of animals that has been omitted from the food-web calculations that produced the pyramids. The only likely candidates for this animal group are jellyfish and other gelatinous animals.

This explanation is likely to be the correct one, or at least to be an important contributing factor. Jellyfish and other gelatinous animals (including salps; Section 8.6) are increasing in abundance worldwide. Having said that, it is interesting that one of the scenarios put forward to explain the continued collapse of the Canadian cod stocks involves a large-scale removal of biomass as a result of long-term overfishing (Section 11.3.4).

The effect of loss of large predatory fish on non-target species

If the stocks of large predatory fish are declining, what is happening to the stocks of other (non-target) species that compete with them or are their prey? At first sight it would seem that these other fish would benefit.

One example of this situation occurred in the long-line fishery for 'billfish' (fish with long 'beaks') in the tropical Atlantic. Initially, blue marlin was the main

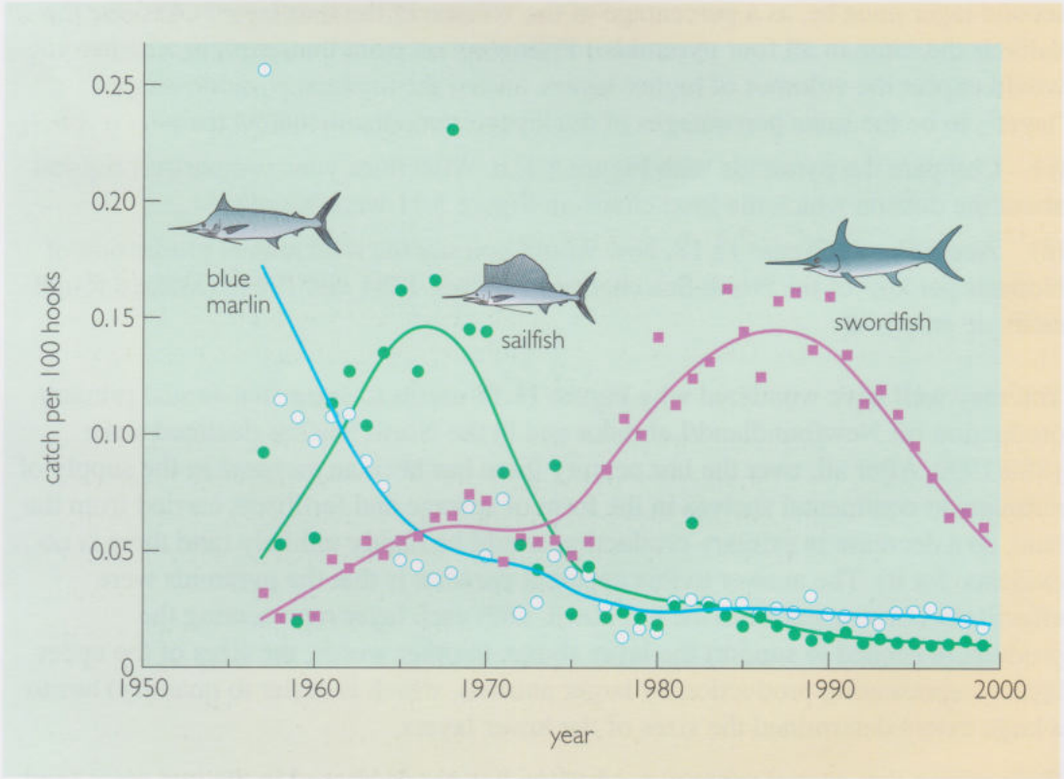


Figure 11.19 Long-line catches of billfish in the tropical Atlantic, showing the catch per 100 hooks of blue marlin (*Makira nigricans*) (open circles, blue line), sailfish (*Istiophoris platypterus*) (green circles, green line) and swordfish (*Xiphias gladius*, purple squares, purple line). You may recall that a marlin and a sailfish appear in 'Open Ocean' (sequences 1 and 4), respectively.

species caught, but from the 1950s onwards catches declined as blue marlin populations shrank. Figure 11.19 shows how the continued decline in blue marlin catches between the 1950s and 2000 was accompanied by changes in the catches of faster-growing species, such as sailfish and swordfish.

Does Figure 11.19 support the idea that populations of sailfish and swordfish benefited from the decline in the blue marlin population?

No, at least not in the long term. Although both species did show increased catches, the catches peaked and then declined.

It is thought that sailfish were increasingly caught as by-catch (they were not targeted by the Japanese long-lining fleet in the area). By contrast, the increase in swordfish catch rates meant that by the late 1980s they had become prime targets of other fleets. Surprisingly similar patterns of 'compensatory increase' followed by decline have been observed in most pelagic communities. It has also occurred in demersal communities in the North Atlantic.

11.4.2 Other long-term side-effects of overfishing

Only very recently have we recognised that fish populations have changed markedly since they began to be exploited by humans – and not just since the beginning of commercial fishing. Archaeological evidence on the eastern side of the Atlantic shows that several thousand years ago prehistoric hunters were catching a wider variety of fish than are caught at the present time; in waters off parts of northern Asia there were 40% more species around than there are now, and the salmon and sturgeon caught were larger. Likewise, ancient middens (rubbish heaps) in the Mediterranean contain the remains of more kinds of fish, and larger individuals, than are found in the area today. Some of the changes in fish populations could have been related to climatic/environmental changes (as has probably occurred over the Canadian continental shelf; Section 11.3.4), but fishing can also play a direct role in unexpected ways.

Permanent changes in fish size

As discussed earlier, fishing tends to remove the largest individuals, and efforts are made to spare smaller, immature fish so that they can grow to breeding age. However, it seems that in exploited populations, removal of larger individuals is leading to a decline in the size of individual fish.

If a population of organisms suffers a catastrophe of some kind (e.g. over-exploitation) so that relatively few individuals survive, those individuals are of course the source of genes for their descendants. As the individuals of the smaller population together provide a smaller gene pool, their descendants are more similar genetically than were individuals in the original large population. Larger fish are likely to be faster-growing individuals, so removing them from the population leaves behind a larger proportion of individuals that are relatively slow-growing. In other words, there is a selection pressure favouring slower-growing individuals. Furthermore, as fish of a given age are smaller than previously, they are maturing at a smaller size, which results in fewer, smaller, eggs per female and a lower fertilisation rate.

These changes in fish size are effectively permanent and, what is worse, they seem to be accompanied by declines in the overall biomass of overexploited ecosystems – you may remember that this effect is suspected in the exploited ecosystem over the

Grand Banks (Section 11.3.4) and could also have occurred in the North Sea (Figure 11.18). Interestingly, there is also experimental evidence that the converse is true, i.e. that removal of the *smallest* individuals results in an *increase* in biomass. Our strategies for restoring fish populations currently take no account of these effects. So, should we be looking for ways to prevent the largest individuals from being caught – or of providing 'safe havens' where fish could grow to 'old age'? Developments relating to the latter idea will be discussed in Section 11.6.2.

Evidence for depletion of the gene pool

The largest fish are very often the most genetically diverse, so their removal has a disproportionate effect on the size of the gene pool. The fact that commercial fishing can seriously reduce the genetic diversity of fish populations was first demonstrated in the case of the orange roughy ('Deep Trouble', sequence 4). The orange roughy is a deep-water fish which is widespread in the North Atlantic, the Indian Ocean and south-west Pacific. Little was known about it and it was once thought rare; but the discovery of large spawning aggregations around seamounts near New Zealand led to the development of a commercial fishery there in the 1980s. Over the course of four years, the catch increased by perhaps 500 times, and by 1990 the biomass of orange roughy at three fishing grounds near New Zealand had shrunk by 60–70%.

Like most deep-water fish, orange roughy are long-lived – as mentioned in 'Deep Trouble' they can live for ~150 years; they grow slowly, and mature late, at around 25–30 years old. As you will appreciate, this means that fishing will remove many individuals before they have had a chance to breed, so there are fewer young to replace those that are caught. Furthermore, if the fish are as old as 25 years before they can breed, they are also relatively large, so even using larger-meshed nets may not allow enough immature fish to escape.

11.4.3 Fishing far and wide, and deep

As fishing grounds relatively close to land are depleted, it is becoming financially worthwhile for the fishing industry to exploit environments that were previously considered too remote. As discussed earlier, this is threatening stocks of certain deep-sea fish, especially as many of the new target species (e.g. Patagonian toothfish and orange roughy) seem unlikely to be able to support a sustainable fishery, because they have long natural life-spans and slow growth rates. Not surprisingly, many deep-water fisheries are poorly managed, and as discussed in Section 11.3.5, may be disastrously affected by illegal, unreported and unregulated (IUU) fishing.

Deep-sea sharks are particularly vulnerable to overexploitation.

- Thinking back to Section 6.1, can you suggest why this might be?
- Shark are elasmobranchs, which (in contrast to teleosts) produce small numbers of young.

Furthermore, many deep-sea members of the shark family are *oviparous*, i.e. the mother gives birth to young sharks, and (unlike the dogfish shown in 'Seasonal Seas', sequence 13) does not release eggs. Members of the shark family have long gestation periods – for example, the spiny dogfish has a gestation period of two years, culminating in the birth of 2–5 offspring. This means that females have a good chance of being caught when they are pregnant, in which case two generations are killed at once. Populations of spiny dogfish are thought to have diminished by more than 85% in areas where it is being exploited.

Fishing in the deep sea, far from land, is of particular concern.

- Can you suggest why this might be, bearing in mind what you have read about the Law of the Sea (Section 11.2.3)?
- Such waters are outside the EEZ of any state, so enforcement of sustainable fishing practices is very difficult. (Remember that a state is legally bound to use its EEZ for conservation as well as exploitation.)

Bottom trawling is now undertaken as deep as 2000 m. Trawling outside of EEZs (i.e. on the high seas) takes place on seamounts, ocean ridges and plateaux, and also along the continental margins where they extend beyond 200 n.m. from the coast. As you have seen in 'Deep Trouble' (sequence 5), bottom trawling is extraordinarily destructive – for example, on seamounts it can destroy up to 90% of the coral cover and the community it supports. Fishing on previously unexploited parts of the sea-bed is destroying the remaining refuges of already heavily overexploited fish stocks, and is damaging unique communities of bottom-living organisms, such as deep-water corals, and their associated fauna (Sections 7.1 and 10.3, and sequence 7 of 'The Deep'). Destruction of these deep bottom communities is not always accidental: fishermen have been known to 'improve' fishing grounds by dragging chains across the bottom, to smash up corals so that their nets do not get snagged on them, and to destroy sponges which would otherwise fill up the nets.

High seas bottom trawl fisheries are currently unregulated and are nearly all conducted in an unsustainable manner, with serious problems regarding misreporting and under-reporting of catches. In 2002, the United Nations General Assembly called upon the international community to address the threats to the biodiversity of communities on seamounts and other vulnerable deep-sea ecosystems as a matter of urgency.

At present, the largest part of the bottom trawl catch is taken in a relatively small area in the north-western Atlantic, in the international waters (> 200 n.m. from the coast) over the shelf and slope of the Grand Banks and the nearby Flemish Cap. It also takes place in more extensive fisheries in the north-eastern Atlantic Ocean, the south-western Indian Ocean and the south-western Pacific Ocean.

About 80% of the high seas catch of bottom species (demersal fish, prawns etc.) is caught by bottom trawling (the rest are caught by bottom long-line and gill-net fishing, i.e. using 'anchored drift nets'; Box 11.1), but bottom trawling in high seas waters is still limited: worldwide, it probably supports no more than a few hundred fishing vessels, out of a total of about three million. The global catch from bottom trawling reported in 2001 was of the order of 200 000 tonnes, which corresponds to about 0.2% of the ~ 83–84 Mt caught globally. The economic significance of the catch is correspondingly small, with a value estimated to be of the order of 0.5% of the global marine fish catch. Furthermore, most of the catch of high seas bottom trawl fisheries is destined for high-value markets in the EU, the USA and Japan, and does not form a vital food supply for any vulnerable population.

All this means that – in theory at least – it is still possible to implement international management measures to protect deep-sea ecosystems. Many marine biologists believe that there should be a moratorium on deep-sea trawling before it is too late – as it may already be for some other ocean ecosystems.

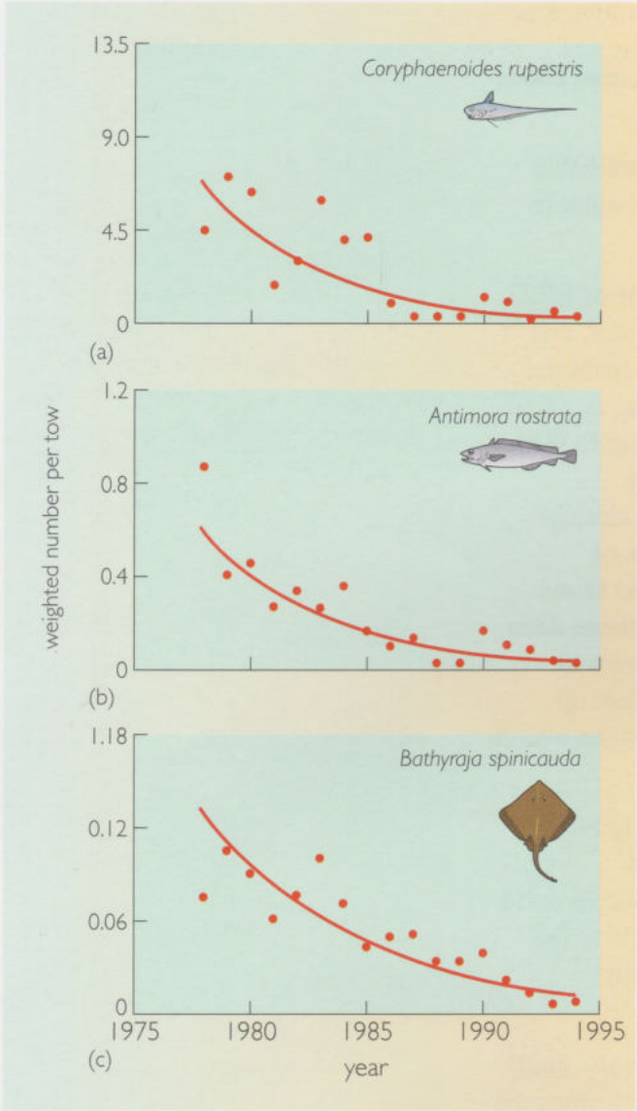


Figure 11.20 Graphs to show the trends in abundance of three deep-sea fish, caught in Canadian waters of the north-western Atlantic between 1978 and 1994: (a) *Coryphaenoides rupestris* (roundnose grenadier); (b) *Antimora rostrata* (blue hake); and (c) *Bathyraja spinicauda* (spinytail skate). (The 'weighted number per tow' is the average number of fish caught over a series of research tows, adjusted to take account of differences in the sizes of the areas fished during each tow.)

Question 11.5 Figure 11.20 shows recently analysed data on the abundance of three deep-sea fish species, caught by bottom trawling over the continental slope in the north-western Atlantic. None of these species were taken in any numbers, even as by-catch, prior to the 1970s. Does anything strike you about these curves? What is their message as far as protection of deep-sea ecosystems is concerned? ◀

It seems that by effectively eliminating many species from the waters over the continental shelf and slope, we human predators are having a similar effect to that caused by the arrival of the Palaeozoic and Modern marine faunas, discussed in Section 1.1!

11.5 The influence of climate change

Fish populations, and the related fortunes of fishing fleets, have always been strongly influenced by the effect of climatic fluctuations. The movements of herring stocks, which so affected the balance of power within Europe for hundreds of years, were certainly influenced by changes in the marine environment (although of course this was not appreciated at the time).

The climatic fluctuation that most affects environmental conditions over the northern North Atlantic and its adjacent seas (as well as north-western Europe), over time-scales of a few tens of years, is the North Atlantic Oscillation, or NAO. The NAO is the continual oscillation in the difference in atmospheric pressure between the area of low pressure over Iceland (the 'Iceland Low') and the area of high pressure over the Azores (the 'Azores High') (cf. Figure 5.1). The greater this pressure difference, the stronger the westerlies blowing across the Atlantic.

As Figure 5.1 indicates, the difference in atmospheric pressure between the Iceland Low and the Azores High varies over the course of the year, and is greatest in winter. This pressure difference is often expressed in terms of an NAO Index, which is positive when the pressure difference between the Iceland High and the Azores Low is relatively large, and negative when the pressure difference is relatively small. The NAO Index of greatest interest is that for winter months, because it is in winter that the NAO has the most influence on the climate. Since the late 1970s, the NAO Index for winter months has generally been positive, which has meant strong westerlies blowing across the Atlantic, with the result that the Gulf Stream and the North Atlantic Current (Figure 5.2) have on average been stronger than usual, with their paths further north, all of which has resulted in a warmer, wetter climate for north-western Europe.

The state of the NAO not only affects the positions of ocean currents and fronts (with their associated high productivity), but also the distributions of water masses, with their characteristic temperatures, salinities, nutrient concentrations and, critically, plankton populations (Section 5.4). However, we cannot be sure of the extent to which observed alterations in marine ecosystems in the North Atlantic area are a result of changes in the NAO because these changes are superimposed on the effects

of global warming, and it is difficult to separate the two. Nevertheless, there is no doubt that seawater temperatures are rising as a result of global warming: the waters around the British Isles are on average about 0.5 °C warmer than they were in the 1870s. The rise in sea-surface temperature has not been uniform: Figure 11.21, which shows temperature change between 1981 and 2000, indicates that most warming has occurred in the southern and eastern North Sea.

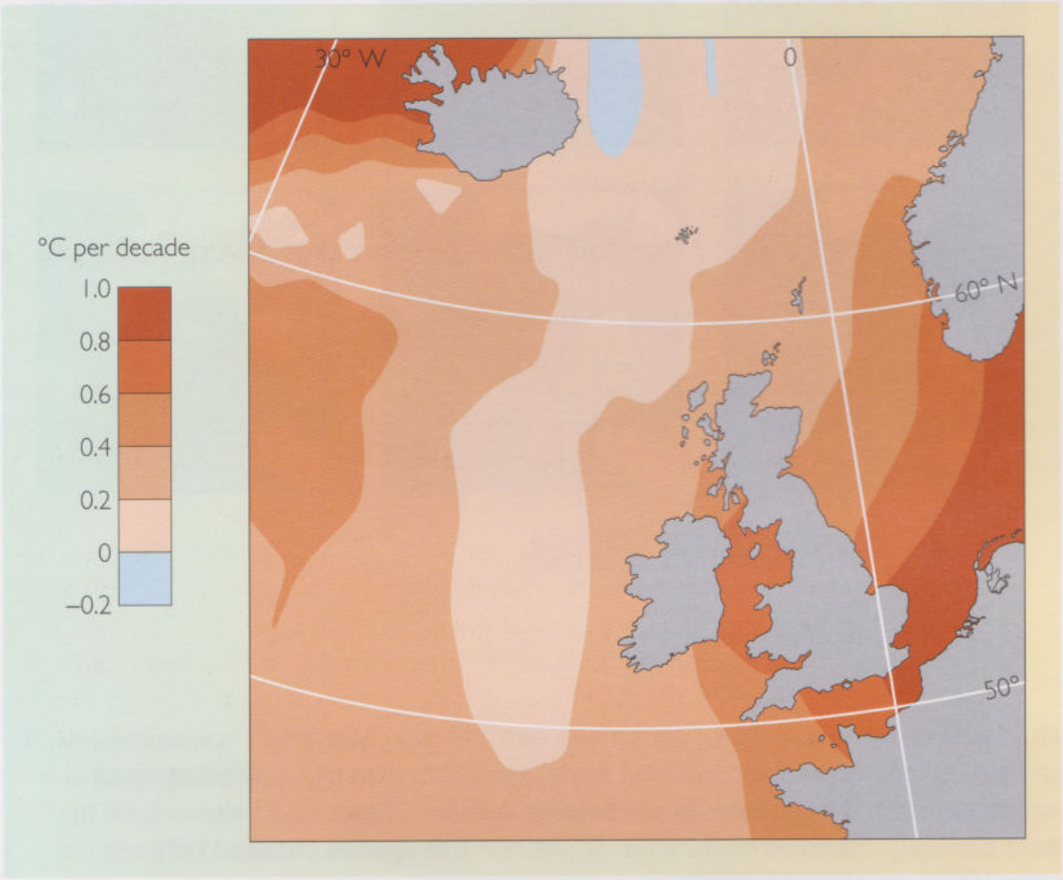


Figure 11.21 Changes in sea-surface temperature around the British Isles between 1981 and 2000. Red tones indicate warming, and blue indicates cooling. Note that the key shows the average temperature change *per decade* over the course of 19 years.

Since the middle of the 20th century, there have been considerable changes in many ecosystems around the British Isles, and there has been a northward movement of warm-water species of plankton, and a corresponding retreat of cold-water plankton, over a distance of more than 10 degrees of latitude. Figure 11.22 shows how the average distributions of four groups of copepods in the north-east Atlantic changed between 1958–81 and 2000–2002. These copepod groups consist of species which tend to be found together as they prefer similar conditions. As you may recall, copepods are extremely common, so even though the maps do not include data on any other groups, they clearly indicate that plankton populations around the British Isles have become typical of warmer water.

Around 1986–1988, there was a marked reorganisation of the ecosystem in the waters around the British Isles, which occurred at the same time as a sharp rise in the temperature of the Northern Hemisphere generally, and a highly positive NAO Index (i.e. strong westerlies and warm, wet conditions in the north-eastern Atlantic).

Thinking back to Section 8.5 and the discussion of the Antarctic food web, can you remember the term used for this type of event (i.e. a pronounced and rapid reorganisation of an ecosystem from one relatively stable state to another)?

The term is *regime shift*.

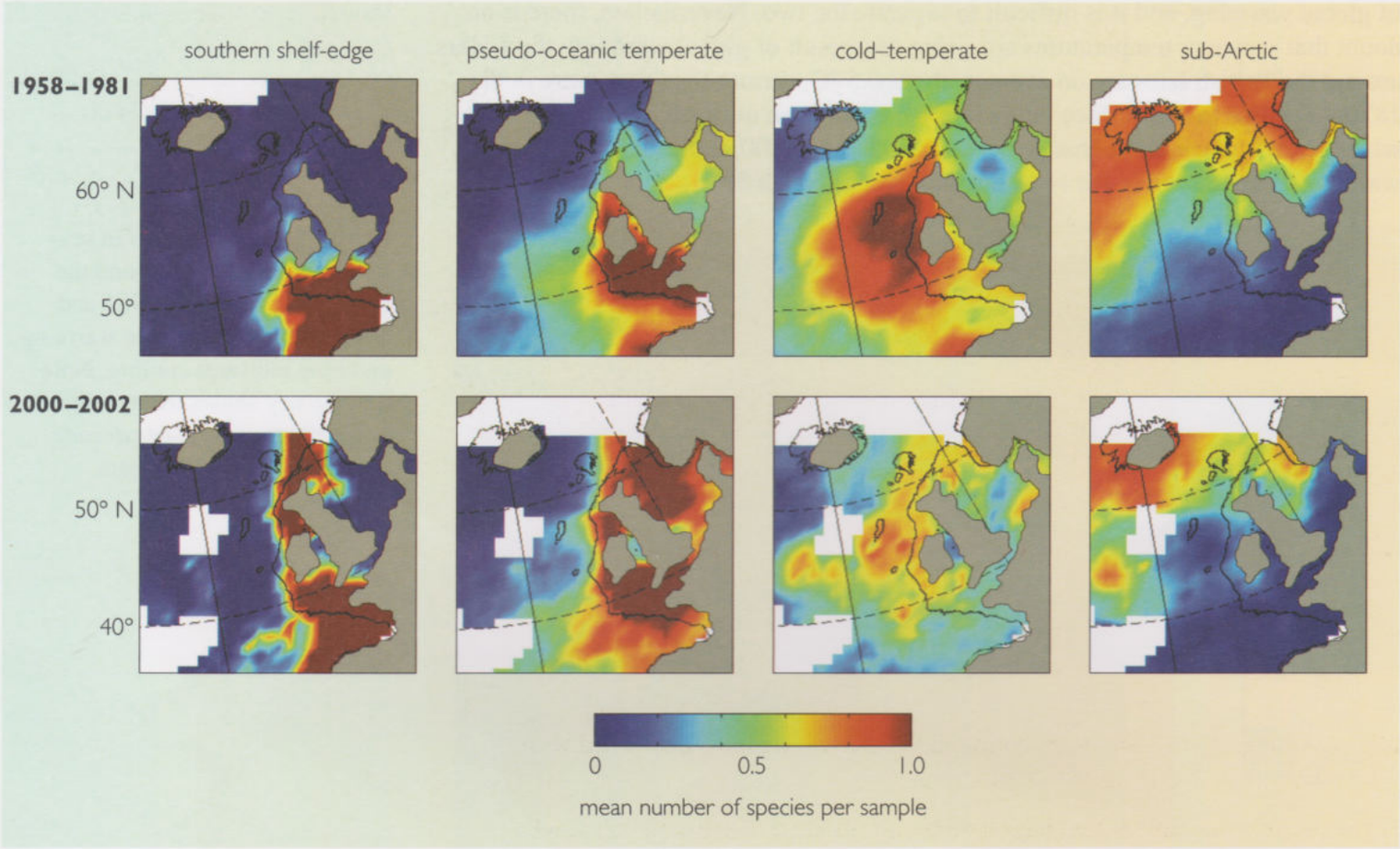


Figure 11.22 Changes in the average distributions of four groups of copepods in the north-east Atlantic, between (a) 1958–81 and (b) 2000–2002. (Do not worry about how the values on the scale bar were calculated. All you need to know is that dark blue corresponds to the presence of very few species of the group concerned, and red to the presence of a large number of species of the group concerned.)

This regime shift was evident not only in nutrient and chlorophyll concentrations, and phytoplankton and zooplankton populations, but also fish (including species caught commercially), seabirds and benthic species. Figure 11.23 shows how the most northerly observed occurrence of just two fish species changed between the early 1960s and the mid-1990s.

Given that 1° of latitude is equivalent to about 110 km, at what average rate did the range of the red dory extend northwards, between 1963 and 1994? (Give your answer in kilometres per year (km y^{-1}).)

Between 1963 and 1994, the most northerly occurrence of the red dory shifted from ~ 36° N to ~ 52° N. This is a northward movement of about 16° of latitude, or $16 \times 110 = 1760$ km, over the course of 31 years, which is equivalent to a rate of 1760 km/31 y $\approx$ 60 km y^{-1}.

The two dory species in Figure 11.23 are just two examples of marine fish whose *biogeographic range* is known to be extending northwards through the waters off north-western Europe. There are many others, ranging from seahorses to sharks, as well as species of crustaceans and molluscs.

To see how subtle the effects of climate on ecosystems can be, let's look at how warming has affected a fish discussed earlier – Atlantic cod, *Gadus morhua*. Because of the influence of the Gulf Stream (cf. Figure 5.2), the waters around the British Isles are considerably warmer than those off north-eastern Canada, even though they occupy a similar latitude range to Newfoundland. Cod are cold-water fish, and are at the southerly limit of their distribution in British waters, so

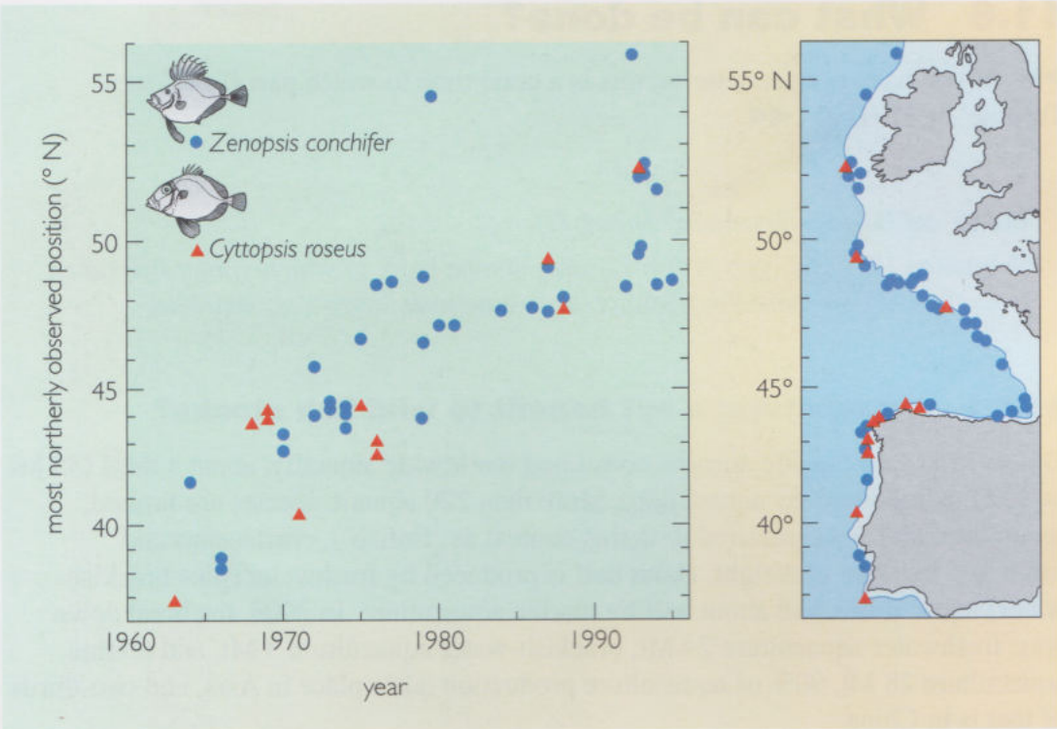


Figure 11.23 The northward movement of the ranges of *Zenopsis conchifer* (silver dory) and *Cyttopsis roseus* (red dory) between the early 1960s and mid-1990s. Both are caught along the edge of the continental shelf of north-western Europe.

it is possible that their abundance around the UK would have decreased with global warming, even without overfishing.

However, it is not simply temperature that has affected overfished cod stocks around the British Isles; as in the waters off north-eastern Canada, it is their food supply. As you may remember, the zooplankton prey species favoured by cod larvae is *Calanus finmarchicus*. This species (which is in fact the favoured food of many fish that are commercially exploited) makes up 70–80% of zooplankton biomass in the northern Atlantic, and is found in abundance over large areas. However, because of the northward movement of cold-water plankton species (Figure 11.22), over much of its previous range off the western British Isles *C. finmarchicus* has been largely replaced by a previously more southerly *Calanus* species – *Calanus helgolandicus*. This species has a different life-cycle from *C. finmarchicus*, and spawns in the summer – too late for its larvae to feed the cod larvae.

More generally, a change in the copepod species composition (i.e. which species of copepods are present in the seawater, and in what proportions) has meant that the mean size of copepods (and their food value) in the waters around the UK has greatly reduced – it has halved since the beginning of the 1980s. Furthermore, older cod larvae and juveniles are also suffering because of a decline in the numbers of euphausiids (the zooplankton group that includes krill). Euphausiids are high in energy, and are an important source of vitamin A, which cod cannot synthesise.

Overfishing may be the primary cause of the decline of cod populations, as in the waters off Canada, but climatic effects are playing a major role in preventing recovery, through their influence on the survival of cod larvae and juvenile cod (i.e. through their influence on *recruitment*). As far as the North Sea is concerned, since the regime shift in the mid-1980s, biological conditions have not been suitable for the growth and survival of larval and juvenile cod.

11.6 What can be done?

▶▶ If you have not yet done so, this is a good time to watch part II of 'Deep Trouble' on DVD 3. ◀◀

Note on 'Deep Trouble' (part II)

Sequence 10 The type of fish-farming shown here, in which young fish taken from the wild are raised to adulthood, is sometimes known as 'ranching'.

11.6.1 Aquaculture: a net benefit to wild fish stocks?

Of the 150 Mt of aquatic animals consumed worldwide annually, about a third (55 Mt in 2003) is produced by aquaculture. More than 220 aquatic species are farmed, including fish *per se* (referred to in this context as 'finfish'), crustaceans and molluscs. In terms of weight, about half is produced by freshwater (plus brackish-water) aquaculture, and about half by marine aquaculture. In 2003, the breakdown was: freshwater aquaculture 24 Mt, brackish-water aquaculture 3 Mt, and marine aquaculture 28 Mt. 90% of aquaculture production takes place in Asia, and two-thirds of that is in China.

Currently, marine aquaculture is relatively undeveloped, and relatively few marine species are farmed. However, as wild fish stocks decline, and the world population grows, we can expect marine aquaculture to play a progressively more important role in providing protein – indeed, aquaculture is often seen as the solution to the problem of overfishing. But to what extent does the production of fish by aquaculture actually take the pressure off wild fish populations in the ocean?

Before moving on, take a moment to study Figure 11.24, which summarises the main ecological interactions between aquaculture, fisheries and the marine environment.

What does Figure 11.24 show to be the greatest ecological impact of aquaculture on the marine environment?

If you are not sure what this is, it will be clear by the time you have read the next section!

Feeding farmed fish

The type of fish-farming that is most familiar to those of us in the British Isles is salmon farming, now a widespread commercial activity in the sea lochs of north-western Scotland. In salmon farming, all the nutritional requirements of the fish are met artificially, which means that they can be kept in relatively small cages, as a kind of intensive farming. At the other extreme, there is 'extensive aquaculture', where the fish, molluscs or crustaceans feed naturally, and human intervention is limited to excluding predators and controlling competition. In between the two is 'semi-intensive aquaculture', where extra food is provided.

Farmed freshwater fish are mostly herbivorous, and are reared in cages, tanks or ponds (often integrated into agricultural enterprises) where they may simply feed on naturally occurring plant material. The molluscs that are farmed are high-value bivalves, and are generally farmed along coastlines, either on the sea-bed (in the case of clams) or on structures such as suspended ropes (in the case of mussels), or bags or cages (e.g. oysters and mussels).

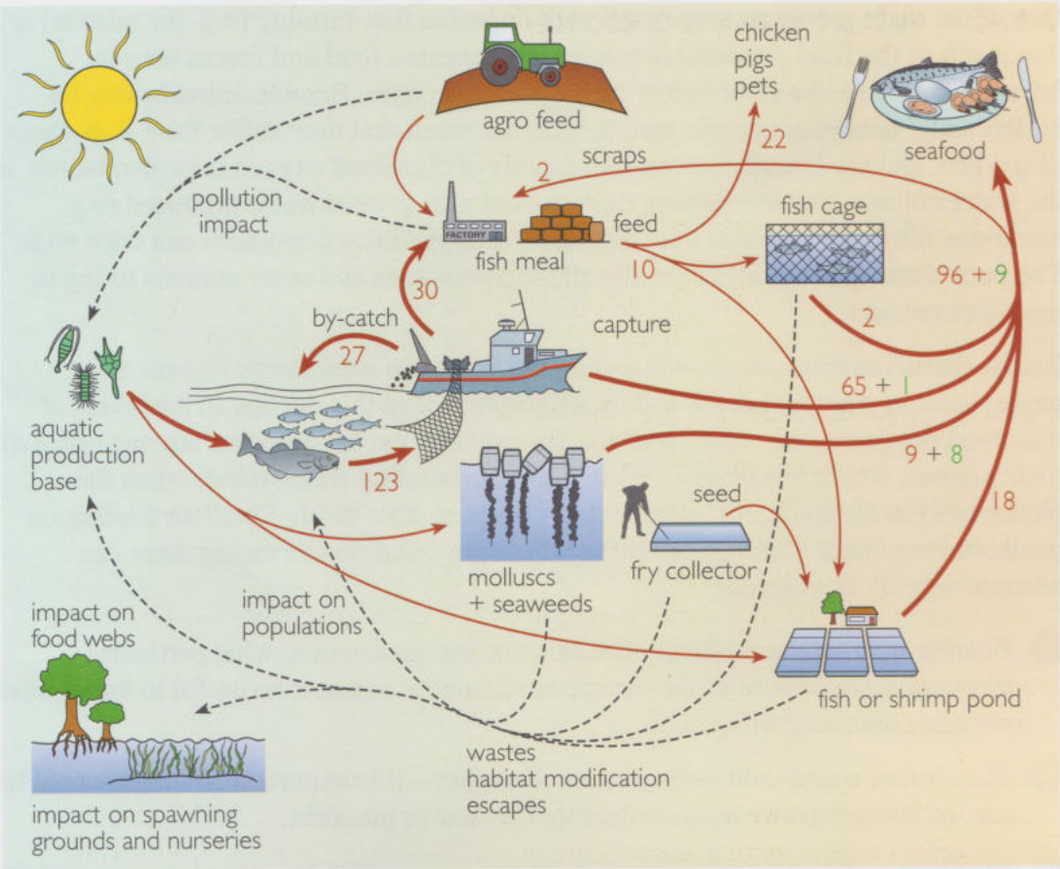


Figure 11.24 Ecological interactions between intensive aquaculture, fisheries and the marine environment. The thick red lines correspond to the main flows from aquatic production, through fisheries and aquaculture, to human consumption of seafood. Numbers are Mt of fish and shellfish (in red) and seaweed (in green) (1997 data). (The annual marine catch of 123 Mt includes by-catch and catch by IUU fishing.) Thin red lines refer to other inputs needed for production. Dashed black lines refer to impacts which have a negative effect on fish production.

What do these animals feed on?

These are all suspension feeders, filtering phytoplankton and organic debris from the surrounding water (Section 3.3). They do not need to be provided with extra food.

By contrast, marine fish, and *diadromous* fish (i.e. fish like salmon or eels, which spend part of their lives in freshwater and part in the sea), are mostly carnivorous. They are generally raised in floating net cages near the shore, and fed with food pellets.

Can you remember what the pellets are made of?

The food pellets are made of fishmeal and fish oil from small pelagic fish like herring, mackerel, anchovy etc. (Figure 11.4).

As mentioned in Section 11.2.1, over half the small pelagic fish taken through industrial fishing are made into food pellets, for use in conventional agriculture (to feed pigs and poultry) and in fish-farming (see Figure 11.24). In intensive and semi-intensive fish-farming generally, for every kilogram of fish protein produced, 2–5 kg of protein has been supplied as food in the form of fishmeal; for most farmed marine fish (flounder, halibut, sole, redfish, seabass etc.), the amount is about 5 kg, and for salmon it is about 3 kg.

In the North Sea, industrial fishing for sand-eels, capelin and Norway pout, mainly for use in aquaculture, has been unremitting. The loss of these small fish from the ecosystem is widely blamed for the decline in larger fish like cod, and for the decline in populations of seals and seabirds: at the time of writing, 2004 was the worst year on record for seabird colonies around the British Isles, with some failing to produce any offspring at all.

One of the main problems associated with intensive fish-farming (e.g. for salmon) is that much of the food provided is wasted, and uneaten food and faeces tend to accumulate on the sea-floor below and around the cages. Benthic animals may be buried under decaying organic matter, with the result that they suffer from a shortage of oxygen, and are literally smothered. Levels of dissolved oxygen may also be low in the water column, and the amount of dissolved nitrogenous waste produced (e.g. ammonia, nitrite and nitrate) may be greater than the local ecosystem can cope with. The poor water quality can adversely affect crustaceans and other animals living in the water column.

Excess dissolved nitrogenous waste (i.e. nutrients) can cause large blooms of phytoplankton which on death and decomposition lead to a decline in the levels of dissolved oxygen in the water; it is also thought that excess nutrients are one cause of *toxic blooms*, which release poisons into the surrounding water, either when the phytoplankton are living, or when they decompose after death. Shellfish feeding on plankton from these blooms concentrate the toxins, and people eating them can become very ill, or even die.

Bearing in mind the problem of excess nutrient production, what particular physical characteristic of the marine environment would it be useful to know when planning the siting of a fish farm?

The current speeds and turbulence of the water – it is important for the waste to be carried away from the area, and diluted, as fast as possible.

By definition, fish being produced by intensive aquaculture are close together, and the problems of dispersing waste are exacerbated if the fish are overcrowded. As in intensive rearing of (say) pigs, disease is more likely to spread under crowded conditions, and pathogens – bacteria, viruses or parasites – could spread to wild fish populations. Farmed fish are therefore given antibiotics and other drugs; this has led to another concern, i.e. that these substances tend to leak out into the environment, and could lead to drug-resistant pathogens.

One of the most widely publicised problems associated with salmon-farming has been heavy infestations of farmed salmon by sea-lice, which has been blamed for increases in sea-lice infestations of wild salmon. Sea-lice are naturally occurring parasitic copepods (Figure 11.25), part of the marine zooplankton community (only the adult stage of their life-cycle is parasitic), and in the past their occurrence on wild salmon was thought to indicate that the fish had recently been to sea.

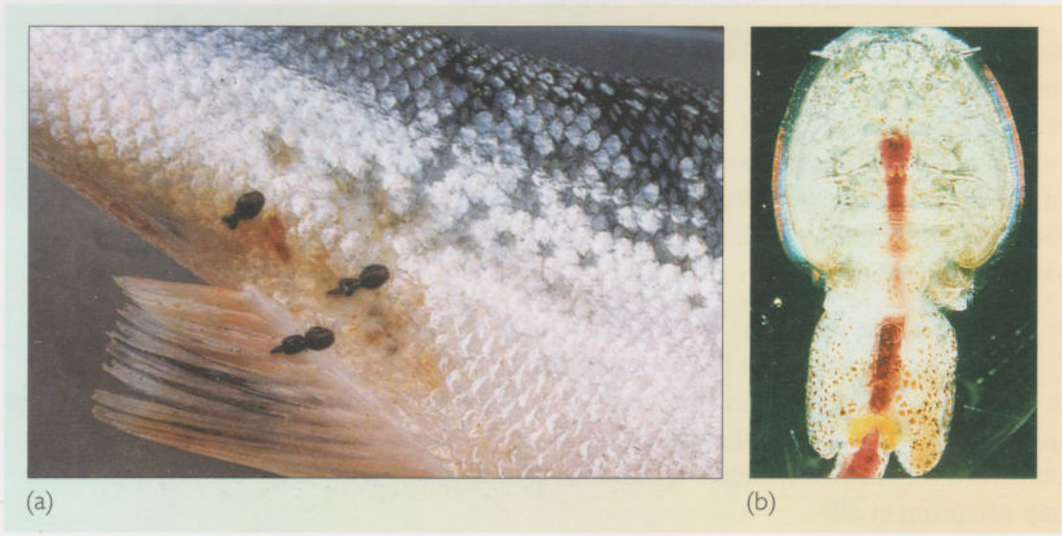

(a) (b)

Figure 11.25 (a) Sea-lice on a wild salmon; the lice are a few millimetres long. (b) Sea-louse with a blood-filled gut. Sea-lice feed on the salmon's mucus, tissues and blood, and a heavy infestation can lead to reduced growth, secondary infections, unsightly lesions, and ultimately early death. The sea-lice problem is being addressed through more effective drugs, aided by research into how young planktonic sea-lice are dispersed in the natural environment.

'Biological pollution'

Causing an increase in the number of sea-lice larvae in nearby waters could be described as 'biological pollution'. Another kind of biological pollution occurs when farmed fish escape; this is a surprisingly common occurrence, and can be a result of storms, accidents or equipment malfunction, and even vandalism and sabotage. Sometimes, it is the result of sea mammals or large predatory fish making a determined effort to get at the farmed fish. In the case of salmon, it is thought that as many as 40% of the salmon caught in the North Atlantic could be escapees, and the situation is similar for the northern North Pacific. Estimates for British Columbia alone indicate that between 1990 and 2000 an average of 90 000 salmon escaped every year – and these salmon were mainly Atlantic salmon (*Salmo salar*) rather than any of the five species of Pacific salmon (genus *Oncorhynchus*), as the former are easier to farm.

Question 11.6 Escaped farmed fish are obviously going to interact with the wild environment in various ways. Make a list of as many potential impacts as you can, and consider whether these are positive or negative for the marine ecosystem. (Try to think of at least *three* impacts.) ◀

Yet another kind of biological pollution that can result from aquaculture-related activities is the introduction of so-called alien species – i.e. species which are outside of their natural geographic range. Some alien species are introduced accidentally, perhaps attached to shells of oysters or mussels supplied for restocking. Some aliens have been introduced intentionally, by operators mistakenly under the impression that they could not breed. For example, in the 1970s Dutch and German oyster farmers began to cultivate the Pacific oyster (*Crassostrea gigas*) in coastal waters of the North Sea. It was assumed that because these oysters are native to Japan, they would not able to reproduce so far north. However, over recent decades there have been massive spawnings from the farmed oysters, and their larvae (or 'spat') settle on any hard substrate in the vicinity. Unfortunately for the blue mussel (*Mytilus edulis*), the spat seem to favour blue mussel banks, which are steadily being transformed into oyster reefs. Such events are likely to become more and more common, as the waters of the North Sea become warmer (Figure 11.21). (It should be said that aquaculture is not the most common cause of species spreading to 'foreign' waters; many are carried as larvae in ships' ballast waters, which are taken on in one part of the world and released in another.)

Now let's move from the North Sea to warmer waters.

Question 11.7 Thinking back to 'Deep Trouble', can you suggest a negative effect that is particularly (though not uniquely) associated with the intensive rearing of high-value crustaceans in coastal environments in the tropics? ◀

Globally, hundreds of thousands of hectares of mangroves have been destroyed to accommodate aquaculture ponds, particularly for milkfish (an herbivorous species) and shrimps/prawns. The problem is particularly severe in South-East Asia, where a third of the world's mangrove forests are found – in Thailand, for example, as much as 50% of the mangrove forest has been destroyed by aquaculture and other human activity. On the basis of statistics collected for Thai mangroves and coastal waters, it has been calculated that loss of nursery beds, and loss of resident fish in the general area of the ponds, means that for every kilogram of farmed shrimp produced, about half a kilogram of wild fish is lost. If we include the negative effects on the

productivity of other coastal marine ecosystems – notably coral reefs (where 10% of fish consumed globally is caught, and much more in developing countries) but also seagrass beds – the net productivity of the ponds becomes low. And that is *without* taking into account the pelagic fish used in artificial shrimp food.

Bearing in mind that mangrove roots bind coastal sediment, and prevent it being eroded, can you suggest yet another reason why the destruction of mangroves causes problems for coral reefs and seagrass beds? (*Hint:* Think back to Chapter 7.)

As discussed in Section 7.2, corals can only flourish in clear waters because their zooxanthellae need light to photosynthesise. Turbid water over a reef, resulting from large amounts of sediments carried offshore from an eroding coastline, will eventually result in the death of the reef. Seagrass beds also suffer if the seagrass does not get enough light to photosynthesise.

Like saltmarshes in temperate latitudes, seagrass beds and mangroves act as 'buffer zones' which protect coastal land from the sea by absorbing wave energy, and their loss can put human populations more at risk from high seas resulting from storms and hurricanes. During the Asian tsunami in late 2004, the destruction, and numbers of human fatalities, were much greater in areas where mangroves had been cleared.

There is no doubt that – particularly in the tropics – land will continue to be cleared to make way for aquaculture ponds for raising shrimps/prawns and fish.

According to Figure 11.24, how does the weight of seafood produced annually in aquaculture ponds (fish and shrimp) compare with that raised in cages sited in coastal waters (fish)?

Figure 11.24 indicates that 18 Mt of fish and shrimp are produced annually in aquaculture ponds; this is nine times the weight produced by raising fish in cages in coastal waters.

There is another, less obvious, reason why aquaculture may have a destructive effect on wild populations of marine animals. Many aquaculture operations are stocked with 'fry' (i.e. juveniles) taken from the wild, rather than raised in a hatchery; and the way in which the fry are obtained can be extremely wasteful.

Let's look at just one example amongst many – tiger prawns. Since the early 1990s, in a number of tropical countries, tiger prawn aquaculture has been expanding as the offshore tiger prawn fishery fails to keep up with demand from the international market. One of the places where tiger prawns are reared is West Bengal. Although there are a few tiger prawn hatcheries, and biotechnology research is being undertaken to support them, many prawn farms depend on the collection of wild fry, and around 50 000 landless rural labourers rely on fry collection as an important source of income. Unfortunately, for every 160 fry netted from coastal waters, only *one* is a tiger prawn, and the remaining unwanted shrimp and fish fry are discarded and left to die on the beach. The annual fry by-catch associated with three collecting centres in West Bengal has been estimated at between 62 million and 2.6 billion. Thus not only are populations of tiger prawns and other species being depleted by overfishing (with an associated large by-catch; 'Deep Trouble' (sequence 9)), but an enormous number of young of other species are carelessly killed for the sake of the aquaculture industry.

It should be emphasised that not all collection of wild fry occurs in developing countries. Other aquaculture enterprises that rely on this practice include the tiger prawn industry in Australia and eel-rearing in Europe and Japan.

Farming up the food web

Developments in aquaculture are occurring in two different directions, of which the first, exemplified by the farming of large, high-value fish like tuna (shown in 'Deep Trouble', sequence 10), can be summarised as 'farming up the food web'. As populations decline, other large seafish are being considered for farming, and experiments are even being undertaken in the farming of cod.

As mentioned in 'Deep Trouble', attempts are being made to reduce the amount of wild fish being fed to farmed fish in fishmeal and fish oil by increasing the amount of plant material (e.g. oilseeds, soya beans) in their diet. The problem is that carnivorous fish need certain essential amino acids which are lacking in plant materials, as well as fatty acids (commonly referred to as EPA and DHA) not found in vegetable oils. They also need a high-energy food, and use plant material inefficiently. Sources of non-vegetable protein being tried are blood and bone meal, and protein produced bacterially (i.e. using biotechnology).

Unfortunately, dietary information relating to certain species is limited, and manufacturers often 'play safe' and produce feeds with more fish protein than necessary. Even feeds for omnivorous fish such as tilapia could contain 15% fishmeal.

The fishmeal industry has proposed that, rather than dumping it back in the sea, fishing vessels should retain all their by-catch and sell it to producers of fishmeal and fish oil.

- At first sight this seems a good idea, but what undesirable consequences might it have?
- It could reduce the incentive to limit by-catch, and would remove biomass from the oceans – at least dead by-catch is food for omnivores and scavengers, and returns organic material to the ocean.

Farming down the food web

As mentioned earlier, most farmed marine fish are carnivorous, although there are some exceptions: milkfish, mentioned earlier, is one of the most commonly farmed fish in tropical countries. However, progress in 'farming down the food web' is being made by adapting aquaculture practices long used for freshwater fish – that of rearing different species together. For example, in China four of the most commonly produced fish are reared in freshwater ponds together: these are silver carp (which feeds on phytoplankton), grass carp (which feeds on aquatic plants), common carp (a bottom-feeding omnivorous detritivore) and bighead carp (which feeds on zooplankton). As the four species exploit different resources, this arrangement maximises production from the pond, and so reduces costs. This type of aquaculture is known as an integrated, or polyculture, system.

In marine aquaculture, such systems generally involve growing high-value marine fish and marine plants together. For example, in Chile, salmon are reared along with a species of red alga (*Gracilaria chilensis*) from which agar is produced (agar is a gelatine-like substance on which bacterial cultures are grown).

What are the advantages of this approach for (1) the environment around the salmon cages, and (2) the aquaculture operators?

(1) The excess nutrients in the water around the cages will be used by the red algae to grow. This will improve the quality of the water, and help prevent problems like plankton blooms, especially as the algae are continually harvested.

(2) The operators get extra income from selling the algae, and do not need to worry so much about pollution (prevention of which can be costly).

Other integrated aquaculture enterprises involve growing mussels and seaweeds in wastewater from intensive and semi-intensive aquaculture operations.

Social consequences of aquaculture

In this section, we have been mainly concerned with the implications of aquaculture for marine ecosystems. However, as it is a commercial activity, the way it is conducted has an impact on human populations. On the positive side, aquaculture enterprises provide local employment. On the negative side, aquaculture operations (especially if poorly managed) may have a deleterious effect on coastal fisheries, and hence on the income of those involved in fishing. In developing countries in the tropics, clearing mangroves for shrimp ponds removes the common resource of the mangroves – which had been freely accessible to local people to catch fish to feed their families – and replaces them with an enterprise under private ownership. Furthermore, shrimp/prawn ponds have a limited life. Waste products produced in the ponds are discharged into the surrounding environment, but after only a few years both the ponds and the surrounding areas have become too contaminated, and the operators have to abandon them, leaving the local people with no employment and no mangroves.

There is also another way in which aquaculture has undesirable consequences for poor communities living along coasts in developing countries.

Bearing in mind how artificially raised carnivorous fish and shrimp are fed, can you suggest what this is?

As shown in 'Deep Trouble' (sequence 11), the enormous numbers of low-value pelagic fish that go to make food pellets for farmed fish and shrimp (most of which are exported) reduce the supplies available to local people. This is a serious problem, as small fish like mackerel, anchovy and sardines are a valuable source of protein for low-income communities; and as populations in developing countries grow, the need for inexpensive protein will become greater.

The verdict

So – returning to the question posed at the start of this section – to what extent does the production of fish by aquaculture actually take the pressure off wild fish populations in the ocean? As is probably clear from the above discussion, the answer is that it depends on what kind of aquaculture practices you consider. Freshwater aquaculture does result in 'extra' fish, but it uses enormous volumes of freshwater, which in some areas is becoming a problem.

At present, marine aquaculture as a whole relies so much on wild fish that the 'extra' fish biomass produced is at best small – and many now believe that it

results in a net *loss* of fish. (It has been estimated that from 1997 to 2001, 21 million tonnes of fish were taken from the ocean to supply aquaculture operations.)

Experts in the field do not believe that availability of farmed fish will, on its own, ever take the pressure off wild fish to an extent that would allow wild populations to recover.

11.6.2 The case for marine reserves

You may well now be thoroughly depressed by the seemingly unredeemable state of marine fish stocks and the ecosystems of which they are a part, so let's end on the one ray of hope – marine reserves.

▶▶ If you have not already done so, you should now watch part III of 'Deep Trouble' on DVD 3. Alternatively, you may prefer to watch it when you have read the last few pages of text. ◀◀

Notes on 'Deep Trouble' (part III)

Sequence 12 The Skomer Island National Nature Reserve (NNR) is 1 km off south-west Dyfed, Wales, within the Pembrokeshire Coast National Park, and was established in 1959. It is owned by the Countryside Council for Wales, and provides a protected breeding environment for grey seals and seabirds, including Manx shearwater, puffin, kittiwake, razorbill, fulmar and guillemot.

Separate from the Skomer Island NNR is the Skomer Marine Nature Reserve, which became an officially designated reserve in 1990 (through the *Wildlife and Countryside Act*, 1982). It includes waters around Skomer Island and the Marloes Peninsula on the Welsh mainland, and covers an area of 1500 hectares. Fishing restrictions in the reserve (in 2005, one bylaw banned the taking of scallops by any means) are enforced through Sea Fisheries Committee bylaws. The main fishery in the area is inshore potting (trapping crustaceans such as lobsters), and this is permitted. In 2005, there was a proposal to limit all fishing in the reserve (commercial and recreational), with the aim of establishing a 'No-Take Zone' (NTZ) in part of the reserve over the next 10–15 years; this was rejected by the South Wales Sea Fisheries Committee. This small case study demonstrates the extreme weakness of UK legislation for protecting the marine environment.

In recent decades, a number of countries have established marine reserves, or Marine Protected Areas (MPAs), using criteria established by the World Conservation Union (IUCN*). These criteria relate to the extent to which the area in question is in its natural state, and to its biogeographical, ecological, economic, social and/or scientific importance. So far, all MPAs have been established either in territorial seas (within 12 n.m. of the coast) or in EEZs (within 200 n.m.), and so are under the jurisdiction of a particular coastal state.

One of the countries that has made the most progress in setting up marine reserves is New Zealand. By far the largest of New Zealand's marine reserves are the entire territorial seas of two island groups: the Kermadec Islands, about 1000 km to the north-east in the Pacific; and the Auckland Islands, 450 km to the south of South

*IUCN stands for the International Union for the Conservation of Nature and Natural Resources. The name changed in 1990, but the original well-known acronym is still used.

Island (see Figure 11.26). Both island groups are volcanic (associated with the destructive margin that passes though New Zealand; cf. Figure 2.5), and as the sea-floor slopes down steeply from them, the reserves encompass both shallow and deep waters; the Kermadec Islands reserve also includes seamounts.

The largest of the reserves off the coast of New Zealand itself is that around the Poor Knights Islands to the north (where sequences were filmed for the Blue Planet series). Even this reserve is less than 2000 hectares in area. In other words, these 'mainland' reserves are rather small (together they only make up about 0.3% of the territorial sea around New Zealand), but as Martha Holmes emphasises in 'Deep Trouble' (sequence 12), they are having a significant effect on the abundance of marine life in adjacent areas. A recent study of the effectiveness of 19 marine reserves worldwide found that they consistently improve biodiversity, i.e. the number of species present. As far as fish were concerned, the number of species in a reserve was found to be about 11% higher than outside it. There was also an increase in the abundance of fish, particularly in the case of exploited fish species.

At present, there are only three statutory marine reserves in the British Isles: that around the island of Skomer (see the Notes for 'Deep Trouble', part III); the waters around Lundy, off the north Devon coast in the Bristol Channel (including a No-Take Zone (NTZ), from which no organisms, living or dead, should be removed); and Strangford Lough in Northern Ireland. There are also a number of other 'voluntary' reserves where fishing is banned, including areas off the Isle of Man, and in the Inner Hebrides. A proposal for NTZs to be set up in the North Sea, proposed during negotiations on the reform of the CFP (Section 11.3.3), was opposed by the UK.

In the North Sea, the only areas of sea-bed where benthic communities remain in anything like pristine condition are – paradoxically – along pipelines, and under oil and gas platforms, because these areas have been inaccessible to fishing gear. As a result, there have been proposals that the lower parts of decommissioned oil and gas platforms should be left on the sea-bed and become the centres of small reserves; such structures act rather like reefs, attracting benthic animals and fish; and in any case fishing around them would be hazardous as gear would get snagged. Unfortunately, worries about liability may well thwart such plans: if in the future a vessel is damaged by encountering a decommissioned platform, the owner will be able to sue the oil company for compensation, even if the vessel was operating in the area with the full knowledge that the hazard was present.

The European legislation relevant to marine reserves is EC Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora, commonly referred to as the *EC Habitats Directive*. This Directive focuses on particular habitats and species (terrestrial and marine), identified by individual member states as requiring special conservation measures. If a site is shown to be sufficiently important for the conservation of one or more threatened species and/or to have a valuable but threatened habitat, then it is designated a Special Area of Conservation (SAC). For example, an area recently designated as an SAC is the inner Moray Firth (north-east Scotland), selected on the basis of its population of bottlenose dolphins and its sandbanks. So far, 12 SACs have been selected around the UK, and management schemes for managing and monitoring them (working with relevant authorities and other local partners) are being developed. Eventually, as many as 70 sites around the British Isles may be designated as SACs.

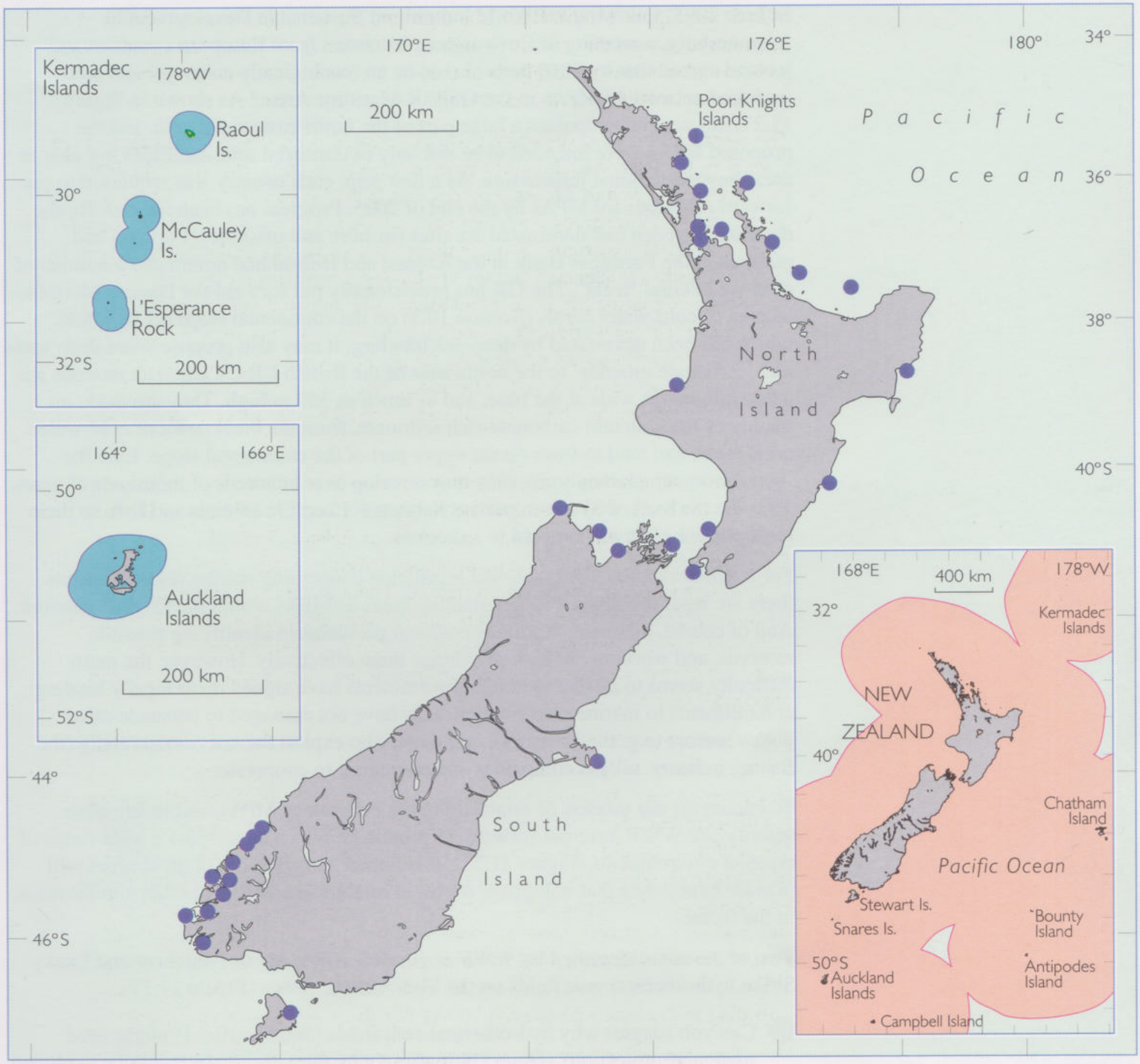


Figure 11.26 New Zealand's marine reserves (blue circles). The total area protected (including territorial seas of the Kermadec Islands and the Auckland Islands, shown in blue) is about 1 million hectares. The pink region in the map at bottom right is New Zealand's exclusive economic zone.

Establishment of SACs, and of marine reserves like those around New Zealand, clearly makes a positive contribution to biodiversity and abundance of marine flora and fauna, and (for reasons which you will now appreciate) coastal reserves are particularly valuable. However, experts now favour a network of MPAs designed to contribute to the protection and recovery of the whole marine ecosystem, rather than focusing on particular habitats and species. It is believed that this approach would be more likely to allow exploited species to recover, afford greater protection to both common and rare species, and result in a healthier environment, more resilient to change (including climate change).

In June 2003, following the World Summit on Sustainable Development in Johannesburg, a meeting of Environment Ministers from European countries and Iceland agreed that by 2010 there should be an 'ecologically coherent' and well-managed network of MPAs in the OSPAR Maritime Area.* As shown in Figure 11.27, this area encompasses a large part of the north-eastern Atlantic, and the proposed MPAs were intended to be not only in territorial seas and EEZs but also in areas beyond national jurisdiction. As a first step, each country was requested to put forward proposals for MPAs by the end of 2005. Progress has been limited. By the deadline, Sweden had nominated six sites (inshore and offshore); Portugal had nominated the Formigas Bank in the Azores; and Ireland had nominated a number of cold-water coral 'reefs'. The UK has provisionally put forward the Darwin Mounds, an area of cold-water corals (Section 10.3) on the continental slope off Scotland, which has been devastated by deep-sea trawling; it may also propose some deep areas and 'carbonate mounds' to the north-west of the British Isles. Carbonate mounds are a few kilometres wide at the base, and as much as 350 m high. They are made up mainly of fine calcium carbonate-rich sediment, from the breakdown of cold-water coral reefs, and tend to form on the upper part of the continental slope. Like the 'reefs' from which they form, they may develop over hundreds of thousands of years; and, like the reefs, they are important habitats for benthic animals and fish, so their locations are often well known to fishermen.

For a number of countries, national legislation concerning marine reserves means there are legal problems with nominating areas as MPAs within the OSPAR network. And of course, there are enormous practical problems in identifying possible reserves, and working out how to manage them effectively. However, the main difficulty seems to be that although governments have signed up to legally binding commitments to marine conservation, they have not managed to persuade other policy sectors (e.g. the Treasury), and those who exploit the sea commercially (the fishing industry, oil/gas companies and shipping), to cooperate.

To encourage the process of establishing the network of MPAs, and to stimulate activity, the WWF have put forward 21 proposals, which encompass a wide range of types of environments (Figure 11.27). It is hoped that adoption of these areas will provide experience that will prove useful in establishing MPAs in other similar areas in the future.

Two of the areas identified by WWF as possible MPAs are the Rainbow and Lucky Strike hydrothermal vent fields on the Mid-Atlantic Ridge (Figure 11.27).

- Can you suggest why hydrothermal vent fields (Section 10.4.1) might need particular protection? (*Hint:* Think about why they eventually might be exploited commercially.)

- Hydrothermal vent fields are sites where there are high concentrations of metals. This is particularly true of black smokers: manganese and iron oxides and hydroxides accumulate on the surrounding sea-floor, and smoker chimneys contain high concentrations of sulfides of iron, zinc and copper (Figures 10.12 and 10.13).

* This is the area defined in the *Convention for the Protection of the Marine Environment of the North-East Atlantic* (1998), also known as the OSPAR Convention because it replaces two former conventions aimed at reducing marine pollution, adopted in Oslo and Paris in 1972 and 1974, respectively.

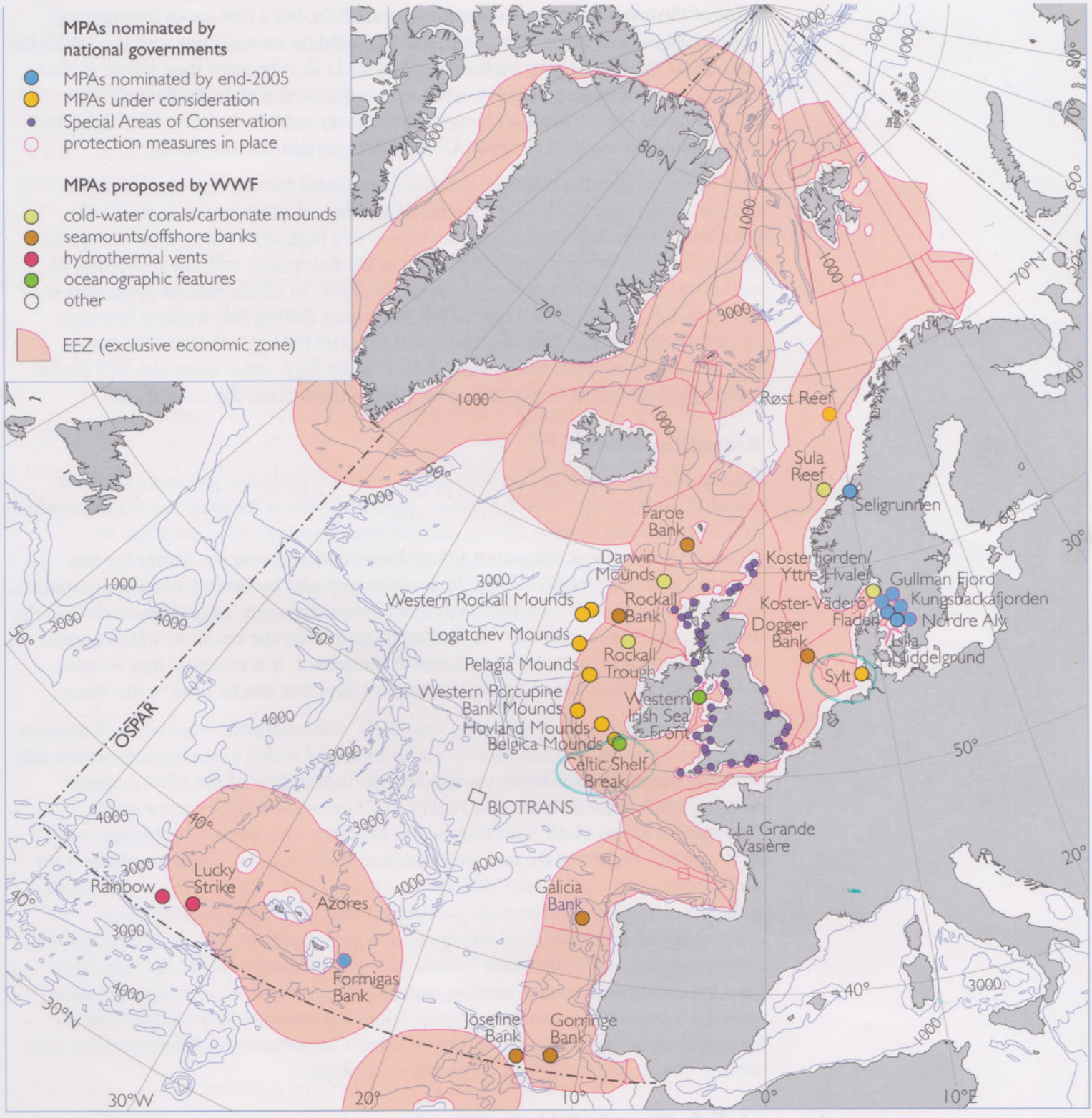


Figure 11.27 Summary map showing MPAs nominated (by end-2005) to be part of the OSPAR network, along with possible MPAs proposed by WWF, in various different environments (see key). Also shown is the location of the Darwin Mounds and some of the possible MPAs around the British Isles (small purple dots) that could qualify as SACs, or already do so (see text). 'BIOTRANS' is explained later in the text. Pink areas are EEZs, and the white strip between EEZs and the coast are territorial seas. Depth contours are in blue.

Most of the areas under consideration are in EEZs, but a few are in international waters. It has been argued that these MPAs would be inconsistent with the UNCLOS concept of 'freedom of the high seas' (Section 11.2.3) because they would exclude fishing, sea-bed mining (e.g. for metal ores associated with hydrothermal vent systems), and waste-disposal. Nevertheless, many experts consider that high seas MPAs could be established under UNCLOS in certain circumstances.

The question remains, however, whether it is lawful for a group of countries to declare a high seas MPA which would be binding on other states. Indeed, one possibility is that the rules governing access to a high seas MPA might be legally binding only on those states setting it up in the first place, with the result that its usefulness could be compromised. Even for MPAs in EEZs, lack of consensus is a problem. For example, Norway, which has strong fishing and whaling interests, claims that protecting deep-sea areas will harm its fishing industry. If Norway refuses to agree to establish protected areas in its EEZ, other countries will find it politically impossible to ban their own fishing fleets from the same areas.

Scientific MPAs

Finally, it's important that certain marine areas are protected primarily for their scientific importance. Nowhere is this more true than in the deep sea. As discussed in Chapter 10 and Section 11.4.3, only relatively recently have we come to appreciate the variety and variability of deep-sea environments. Partly for this reason, and partly because of the restrictions imposed by lack of suitable equipment, we lack long series of measurements and observations (i.e. long 'time-series') in the deep oceans. Now that we are beginning to appreciate the extent to which human activity is impacting on the deep-ocean environment, it is essential that we plan ahead and establish a bank of basic reference data that can be used in the future.

A good example of a potential high seas MPA with scientific value is the 'European Deep-Sea Transect', a band of well-studied sea-bed which extends south-westwards from the Porcupine Sea Bight (marked by the indentation of the 1000 m depth contour, south-west of Ireland in Figure 11.27) across the area known as the Porcupine Abyssal Plain. This transect includes the area where 'Bathysnap' was deployed (cf. Figure 10.6), and an area where ecological investigations have been undertaken since 1984 ('BIOTRANS' on Figure 11.27). An enormous amount of technical, scientific and financial investment has gone into gathering basic environmental and ecological information in this region, by the UK, Germany and other countries of the European Union. Any major disturbance of this long-term research area would lead to massive and irretrievable loss of scientific reference material. Long-term measurements and reference material, such as that from the European Deep-Sea Transect, will be of utmost importance for future research into climate change and its effects on global ecosystems.

11.6.4 Concluding comments

If there is a way of reversing the ecological destruction caused by modern fishing methods, it must involve management of fisheries in the context of the ecosystems of which fish are a part, and serious consideration of the social and economic situation of those who make a living from the sea, along with the political will to bring about change. Science has an important part to play in providing accurate information which might just prevent the continued and (under present circumstances) inevitable collapse of fisheries – but the best advice is of no help if it is ignored.

We must take this issue seriously: for our own good, and for the continued survival of many of the beautiful and amazing organisms shown in the Blue Planet programmes. Only a small fraction of oceanic ecosystems below 200 m have been investigated, but it is clear that the deep ocean is a major reservoir of biodiversity, with estimates of numbers of species ranging between 500 000 and one million.

To quote from a recent report about bottom trawling in high seas waters:

> If the international community cannot prevent the destruction of the wealth of deep-sea biodiversity on the global commons from bottom fishing by a relatively small number of countries and vessels [cf. Figure 11.20], what hope is there that we can halt and reverse the decline of Earth's biodiversity overall for future generations?
>
> *High Seas Bottom Trawl Fisheries and their Impacts on the Biodiversity of Vulnerable Deep-Sea Ecosystems*, by Matthew Gianni (2004)

To round off Chapter 11, attempt Questions 11.8 to 11.10.

Question 11.8 One of the consequences of fishing being a commercial activity, rather than simply a way of obtaining food, is that an enormous quantity of fish is wasted. Make a list of the ways in which fish that could provide food for humans are wasted as a result of current fishing practices. ◀

Question 11.9 The complexities of food-web interactions are very gradually becoming better understood. Perhaps surprisingly, there seems to be a link between the decline in numbers of large, mature predatory fish, and the successful growth and development of young larval fish of different species. Thinking about the implications of a fish being mature, and about the characteristics of teleost fish (Section 6.1), can you suggest what this link might be? ◀

Note: This final question, which requires a more extensive answer, is similar to the type of question which you could encounter in an ECA, and you could use it to give yourself some practice. The question draws on material in Sections 11.2.1, 11.4.3 and 11.6.1, and in parts I and II of 'Deep Trouble'. We suggest that you first make some notes on the basis of what you remember, and then *check your facts* before writing out your final answer.

Question 11.10 Although we have been concentrating on fish in this last chapter, sea-bed invertebrates do not escape the effects of human activities associated with exploitation of the oceans. Briefly discuss how (1) certain fishing techniques (e.g. for cod), and (2) aquaculture enterprises (raising fish and crustaceans), may have adverse effects on benthic invertebrate species. *(Five or six sentences in all)* ◀

Questions: answers and comments

Question 1.1

(a) Corals belong to the Phylum Cnidaria.

(b) Like corals, jellyfish and sea-anemones are cnidarians. Sponges are the least closely related as they belong to a different phylum, the Porifera.

Question 1.2

If you could not guess the answer from the names and the small drawings in Figure 1.5, the answer to this question was to be found in Figure 1.7. The representatives of the Echinodermata illustrated in Figure 1.5 are (1) the Crinoidea and the Stelleroidea (which encompass the Ophiuroidea and the Holothuriodea), and (2) the Echinoidea. Figure 1.5 also shows that Eocrinoidea – early crinoids – were characteristic fauna of the Cambrian.

Question 1.3

The five major mass extinctions indicated in Figure 1.1 show up in the graphs in Figure 1.5 as sharp drops in the numbers of families around the ends of the Ordovician (O on the axis), the Devonian (D), Permian (P), Triassic (Tr) and Cretaceous (Cret). These extinctions show up the most in the graph for fauna characteristic of the Palaeozoic (especially the extinction around the end of the Permian), but they can also be seen in the graph for Modern Fauna (especially the one at the end of the Cretaceous).

Question 2.1

The cross-section in Figure 2.7 does not correspond to any real ocean. An east–west section across the Pacific would have trenches on both sides (and a ridge more to the east than central); one across the Atlantic would have no trench, and relatively wide continental shelves on both eastern and western sides; one across the Indian Ocean would have a central spreading ridge and a trench–island arc system on the east.

Question 2.2

The following are good examples of (1) low-energy coastlines, and (2) high-energy coastlines:

(1) Morecambe Bay, Weston-super-Mare, the coastline around the Wash, and many other estuarine areas.

(2) The coasts of Pembrokeshire and Cornwall, and north-west Scotland; and Chesil Beach near Portland – the ultimate pebble beach!

You may well have thought of other good examples.

Question 2.3

(a) Employing the method used to estimate the speed of the whale, we can read off a speed of between 2×10^{-2} and 3×10^{-2} m s^{-1} = 2–3 cm s^{-1} for a 1 cm-long krill. As with the whale, this is an order-of-magnitude estimate.

(b) A speed of 10 m s^{-1} for a 30 m whale is equivalent to one-third of a body-length per second, while 2 cm s^{-1} for a 1 cm euphausiid is two to three body-lengths per second. These values are generally consistent with the relationship in question (10 body-lengths for the smallest organisms, to one body-length for the largest). Krill are by no means the smallest organisms (bottom of Figure 2.3), and use of the term 'cruising' implies that the whale is capable of swimming much faster than 10 m s^{-1}. As the programmes clearly show, most animals swim with variable speeds, sometimes making sudden fast bursts. For example, some large copepods (which are smaller than krill) can briefly attain speeds of 35 cm s^{-1} (3.5×10^{-2} m s^{-1}).

Question 3.1

(a) High tides resulting from the Moon are 12 hours 25 minutes apart because the (ideal) tidal ellipsoid within which the Earth is rotating every 24 hours is itself also turning, the 'bulges' following the Moon as it orbits the Earth (p.41). In contrast, the tidal ellipsoid caused by the Sun remains effectively fixed, resembling the situation shown in Figure 3.1 (apart from gradual changes resulting from the Earth's orbit around the Sun). As a result, the period between 'solar' high tides is *exactly* half the time it takes the Earth to turn once, i.e. half a day or 12 hours.

Note that the actual tidal cycle is obtained by adding together the tidal cycles of the Moon and Sun, producing somewhat uneven changes in tidal height, as in Figure 3.2. The normal tidal cycle (high tide–low tide–high tide–low tide) is about 24 hours 50 minutes long because the changes in water level due to the Moon are roughly twice the changes in water level due to the Sun, so the lunar tidal cycle is dominant.

(b) (1) At the peak of spring tides, the tidal range in the Tay estuary is about 5.5 m (about 3 m below the 0-line plus about 2.5 m above the zero line). (2) During the smallest neap tides, the tidal range is about 2 m.

Question 3.2

(a) The statement is true. When the Moon is full, there are spring tides; during the following week it moves towards third quarter (Figure 3.2), and neap tides, so the tidal range is decreasing.

(b) When it is New Moon and spring tides for us in Britain, it is also New Moon and spring tides for Australians. The phase of the Moon is the same the world over – for example, a New Moon is observed the world over whenever the Moon is between the Earth and the Sun. Similarly, spring and neap tides occur at the same time wherever you are (although there will be small variations in exact timing, caused by local sea-bed topography and the shape of the coastline).

Question 3.3

Important factors would be:

- the type of substrate (rocky, sandy, muddy);
- temperature (and temperature range);
- salinity (and salinity range);
- how exposed or sheltered the site is;
- how long the site gets exposed to the air during the course of the tidal cycle;
- what predators live nearby;
- whether there is a good food supply for the species in question;
- what competing species there are.

If you thought of all of these factors, you were doing very well.

Question 3.4

(a) The baby crabs return exactly one month after the eggs were laid. This will again be a time of neap tides, as the spring–neap cycle is about a month (actually 29.5 days). The Moon will again be a Half Moon. (The narration says that the eggs are laid during 'the smallest tides of the month', but of course there are actually two periods of neap tides every month.)

(b) There is no obvious answer to this question. One possibility is that if the baby crabs arrive on the beach during a *rising* tide in a neap period, they have the least chance of being carried out to sea again when they are trying to get onto land.

Question 3.5

(a) The surf-riding snails are best described as scavengers.

(b) You may have spotted the following suspension-feeders: the clam (sequences 5 and 6), mussels (sequence 11), barnacles (sequence 11), and brine shrimps (sequence 18). All of these are active feeders.

Humpback whales could also be described as suspension- or filter-feeders, as they strain plankton from the water column. Jellyfish could be described as suspension-feeders (though not filter-feeders).

Question 3.6

(a) (i) Extra-high high tides would occur at a time of extreme spring tides. These would occur during a solar eclipse, because at such a time, Earth, Moon and Sun are aligned *exactly*.

(ii) An eclipse occurs during a time of New Moon (when the Moon is between the Earth and the Sun: Figure 3.2), so 14 days later (i.e. half a lunar month later) there will be a Full Moon.

(b) Normally, kelp grows subtidally (i.e. below the low tide mark) (Section 3.2.2). Here, the entire kelp plants are exposed, so the low tide must be unusually low, indicating a time of spring tides. The Moon at this time must have been either a New Moon or a Full Moon (strictly, just after a New Moon or a Full Moon) (Section 3.1).

Note that if this were an ECA question, and you had answered the first part of (b) by writing about something *other* than the appearance of the kelp, it would not have earned you any credit!

Question 4.1

If the tilt of the Earth's axis increased to 30°, the Tropics of Cancer and Capricorn would be at 30° N and 30° S, and the Arctic and Antarctic Circles would be at 60° N and 60° S respectively.

Question 4.2

Sunlight would penetrate further down through the water column in the open ocean because coastal waters are more turbid, containing larger concentrations of sediment from the land *and* larger concentrations of phytoplankton (cf. Figure 4.1). Coastal waters also contain greater concentrations of dissolved organic compounds, brought in by rivers (cf. the yellowish Baltic water off the coast of Norway in Figure 3.4) and produced by coastal plankton.

Question 4.3

(a) Dark upper surfaces mean that predators above the fishes find it hard to see them, and silvery undersides mean that predators below find it hard to see the fishes against the light coming down from the surface.

(b) Red animals are red because they reflect *only* red light. As Figures 4.6a and 4.7 show, within a very short

distance of the sea-surface there is no red light, so a red animal will look dark or black, along with those that really *are* black, and will be inconspicuous in the gloom. All pelagic shrimp that live below 500–700 m by day are bright red, while those living at shallower depths are transparent or semi-transparent.

Question 4.4

Temperature decreases with depth in the thermocline (by definition). As this has a greater effect on the speed of sound than the increasing pressure, the speed of sound must decrease with depth in the thermocline. Below 1000 m depth, the temperature profile is vertical, or nearly so. A vertical temperature profile means no change of temperature with depth. Therefore, below 1000 m depth (as in the mixed layer), the speed of sound is determined only by pressure. As pressure increases with increasing depth, the speed of sound must also increase with depth below 1000 m (as it does also in the mixed layer). There is therefore a *minimum* in the speed of sound at the bottom of the thermocline/top of the cold deep layer.

Question 5.1

(1) The poleward-flowing warm current in the North Atlantic is the Gulf Stream, and its counterpart in the North Pacific is the Kuroshio; (2) the poleward-flowing warm current in the South Atlantic is the Brazil Current, and (3) that in the southern Indian Ocean is the Agulhas Current. (In the South Pacific, where the western boundary of the ocean is rather broken up, the most comparable current is the East Australian Current.)

Question 5.2

Figure 5.7 shows that Cape Douglas is one of the sites where nutrient-rich Cromwell Current water upwells to the surface, and Figure 5.8 shows that – not surprisingly – this is a site where large algae (seaweeds) flourish. As you saw in sequence 5 of the introductory programme, marine iguanas feed on such algae, so this is a good place for them to live.

Question 5.3

(a) The upwelling region in 'Open Ocean' is that associated with a seamount. The narration refers to currents being deflected up its 'towering walls' which is a reference to the same kind of situation as on the western side of islands in the Galápagos, where filaments of the Cromwell Current are deflected upwards (Figure 5.7). The currents will not be deflected up from the bottom of the seamount, as indicated by the narration. The current responsible for the upwelling must be in the upper part of the ocean, where the wind can have some influence – when the wind shifts, the current (or filament of current) shifts (end of sequence 7), and the upwelling will stop (or be concentrated on a different part of the seamount).

(b) You may have noted down some or all of the following:

Level 1 (primary producers) Phytoplankton (part of the unspecified plankton mentioned at the beginning of the sequence) and seaweeds.

Level 2 (herbivores) Mysid shrimps and juvenile fish; anchoveta. As will be discussed in Chapter 7, small reef fish are typically herbivores.

Level 3 (carnivores consuming herbivores) The blue maomao and trevally, which consume the shrimp and other plankton; the six-month old yellow-fin tuna; white-tip reef sharks; silke sharks; bonito. (For convenience, we can also include here fish that eat the eggs of other fish.)

Note Apart from the mysid shrimps (which are in fact omnivores), we were not told much about the zooplankton. Food chains involving zooplankton are likely to have four trophic levels; there would also be four (or more) trophic levels if (say) dolphins were present, feeding on squid or carnivorous fish (which would include fish that eat zooplankton).

Question 5.4

(a) Using the method illustrated in the text, we have: annual production of baleen whales
$= 50 \text{ MtC} \times 0.12 \times 0.04 = 0.24 \text{ MtC}$.

Adding this to the annual production of piscivorous fish of 0.5 MtC, we get a total annual production of top carnivores of $0.74 \approx 1$ MtC. In terms of live weight, this would be about 10 Mt.

(b) (i) Similarly, for the open ocean food chain, we have: annual production of piscivorous fish/squid $= 20 \text{ MtC} \times 0.25 \times 0.15 \times 0.1 \times 0.1 \times 0.1 = 0.000\,75 \text{ MtC}$.

One megatonne is 1000 kilotonnes, so 0.000 75 MtC = 0.75 ktC.

(ii) The annual total production of top carnivores in an upwelling area could therefore be as much as $\sim 0.74/0.000\,75 \approx 1000$ times that in an area of open ocean of comparable size.

Question 5.5

(a) According to Figure 8.4, the rorqual feeds on herbivorous zooplankton, carnivorous zooplankton, and carnivorous clupeid fish (which feed on herbivorous zooplankton). It is at trophic level 3 when it feeds on

herbivorous zooplankton (which eat phytoplankton), and at trophic level 4 when it feeds on carnivorous fish or carnivorous zooplankton (which eat other zooplankton). (Clupeid fish are soft-finned fish which form schools.)

(b) In 'Open Ocean', we see tuna at different stages of its life cycle: eggs, larval tuna ('hatchlings'), six-month-old tuna, and mature tuna. Being so small, fish larvae can only feed on zooplankton (this includes eggs and larvae of other fish); young tuna eat sardines and other small fish; adult tuna can eat larger fish, which are likely to be higher up the food chain than smaller fish (it's arguable what trophic level eggs are at). This example illustrates how animals often occupy different trophic levels at different stages of their lives.

Question 5.6

(a) (i) The groups of gelatinous zooplankton you may have noted down are:

Jellyfish; Phylum Cnidaria. (These can be seen in: 'Tidal Seas' sequence 14; 'Seasonal Seas' sequence 2; a red deep-sea jellyfish, and *Periphylla*, can be seen in 'The Deep' sequence 5.)

Siphonophores; Phylum Cnidaria ('The Deep' sequence. 2).

Comb jellies (sea gooseberries); Phylum Ctenophora ('The Deep' sequence 2 , 'Open Ocean' sequence 3).

Salps (Phylum Chordata) ('Open Ocean' sequence 5)

Remember that the question asked for two groups of gelatinous zooplankton from at least two **different** phyla.

(ii) Gelatinous animals are transparent or semi-transparent. For those that live in well-lit surface waters or in the twilight zone, this is an advantage because it means they can escape the notice of any predators that hunt by sight. It also means that they can contain symbiotic photosynthesising algae, like the swarms of thimble jellyfish in 'Tidal Seas'.

Being near-transparent means that they can also 'trawl' for prey without being spotted, while being soft/flexible means that they do not give themselves away to potential prey by disturbing the water.

As their bodies are effectively the same density as the water in which they move, they are extremely energy efficient.

(Although there were a range of appropriate points, we only expected you to have thought of two of them. (This part of the question asked for an answer of only one or two sentences).)

(b) As they are so delicate, they are difficult to catch to examine directly (they break up in the nets used to sample plankton). If they *are* caught, they dry out very quickly, so ideally they need to be studied *in situ*, i.e. in the ocean. Many of the mid-water gelatinous animals have only been observed fairly recently (from submersibles). As they break up so easily, and are largely composed of water, they are hard to identify in the gut contents of other animals, and do not leave any visible remains after death. (None of these points are made explicitly in the programmes, but you may nevertheless have deduced one or two of them.)

As shown in 'Seasonal Seas' (sequence 2), they may have complex life-cycles, starting off as polyps on the sea-bed, and transforming into medusae. As suggested in 'Tidal Seas (sequence 14), they have population explosions.

(Again, there were a number of points you could have made, but you were only expected to identify half of them (we asked for an answer of three or four sentences only)).

Question 5.7

The top predator in the Arctic is the polar bear, which appears in the introductory programme. Polar bears prey on belugas and seals, and have no natural predators themselves.

Question 6.1

Visible features that are characteristic of sharks include:

- an asymmetrical tail, with the upper part more prominent than the lower part (we will be discussing this later);
- visible gill slits (there is a particularly clear view of the gill slits of a nurse shark in sequence 16 of 'Tidal Seas');
- tough, flexible skin, rather than scales;
- the jaw hinge is below the body, with the result that the mouth is underneath the snout (in most fish, the jaw hinge is aligned with the 'mid-line').

Question 6.2

The fins in question are as follows: sea-horse – pectoral fin and dorsal fin; stickleback – dorsal and pectoral fins; bowfin – dorsal fin; knifefish – anal fin; John Dory – dorsal and anal fins; sunfish – dorsal and anal fins.

Question 6.3

(1) If the 'gas container' is rigid, its volume stays the same when the animal changes depth, and the lift generated by the gas within it hardly varies. This is an advantage, in that,

there is no possibility of the animal finding itself rising or sinking in the water column as a result of a positive feedback effect, and there is no need to expend energy in continually adjusting the volume of the container.

(2) A serious disadvantage is that because pressure increases with depth, the depth range of the animal is greatly constrained by the strength of the 'box'. For example, cuttlefish cannot go deeper than about 200 m without their buoyancy organ (the many-chambered cuttlebone, covered by a membrane) imploding.

Question 6.4

Tuna have torpedo-shaped bodies which reduce drag, and have small fins along the rear end of the body that may delay the onset of turbulence. Their streamlined shape is enhanced because they have grooves into which they can flatten their fins. Their swimming style is efficient because it involves minimal body movement, with forward thrust provided by powerful tail strokes. The tail itself is of high aspect ratio.

Question 6.5

Sequence 16 of 'Tidal Seas' showed nurse sharks and stingrays hunting for invertebrates buried in the sediment. As discussed in Section 6.1, sharks and rays belong to the Class Chondrichthyes (i.e. they are elasmobranchs).

Question 6.6

Both statements are false. The first is false because as a fish's swimming speed increases, so more white muscle is progressively brought into play ('Swimming in Fish', sequence 2). The second must be false because white muscle is used particularly for *bursts* of fast swimming. After it has been used – by, for example, a salmon leaping a salmon run – the fish needs time to recover (to excrete the waste products produced by anaerobic respiration, or allow them to be oxidised), as discussed in Section 6.4, and in 'Swimming in Fish' (sequence 4). (This point comes up again in 'Wild Moves: Water' (sequence 6).)

Question 6.7

Both mackerel (seen in 'Swimming in Fish') and sharks (seen in 'Wild Moves: Water') have bodies which are more dense than water. To avoid sinking, both need to swim continually in order to generate dynamic lift. The techniques they use to generate dynamic lift have much in common. Mackerel use their pectoral fins and their tails to produce extra dynamic lift (which only comes into play when the fish is moving relative to the water: 'Swimming in Fish', sequence 3). As mentioned in Section 6.3, mackerel also generate lift by swimming at an angle (which is why, when they tire and are swimming slowly, they swim noticeably 'tail down in the water' (sequence 4) – cf. the in-text question about mackerel in Section 6.3). Recent research, described in 'Wild Moves: Water' (sequence 9), suggests that sharks get lift from their asymmetric tail, and swim at an angle to balance this force.

Question 6.8

Marine mammals have not evolved special buoyancy aids because they have air in their lungs (which therefore act as if they *are* buoyancy aids). (The blubber of marine mammals will also help to reduce their overall density.)

Question 6.9

As discussed in'Wild Moves: Water', possible reasons for dolphins' spectacular swimming performance include:

- ridges on the skin stabilise the flowing water and reduce turbulence (turbulence greatly increases drag) (sequence 3);
- the 'three-hinge' motion of the body during swimming, and the flick of the tail at the end of every stroke, together create a lot of power (sequence 3);
- there may be extra storage of energy in the skin and blubber layer, which when released provides extra 'spring' (analogous to the release of elastic energy employed by kangaroos) (sequence 3);
- the habit of 'porpoising' (i.e. leaping out of the water while travelling) is useful for reducing frictional drag with the surface layer of water (sequence 5).

Question 7.1

Temperatures on the western sides of the Atlantic and Pacific are generally higher than they are on the eastern sides at the same latitude. This is because western boundary currents (like the Gulf Stream) carry warm water polewards, while eastern boundary currents (like the California Current) carry cold or cool water equatorwards (Figure 5.2). Water temperatures are further lowered along the eastern sides of the tropical Atlantic and Pacific by the upwelling that occurs there, in response to the Trade Winds (Section 5.2.1). As a result, temperatures conducive to coral-reef growth are found over a much wider latitude range on the western sides of the Atlantic and Pacific than on the eastern sides.

Question 7.2

Butterflyfish are flat, with a rounded outline, corresponding to the fish-shape at the apex of the 'fish triangle' (Figure 6.3). This is the shape best suited to good manoeuvrability, as is the rounded tail.

Manoeuvrability is very useful for swimming amongst the intricate coral 'landscape' and, especially, for evading predators (butterflyfish are not particularly fast).

Question 7.3

According to Figure 6.6, the parrotfish in sequence 4 of 'Coral Seas' have truncate tails (which are for slightly faster swimming than rounded tails, and provide slightly less help in manoeuvring). The parrotfish that can be seen most clearly seems to be swimming by using its pectoral fins like oars.

Question 7.4

The jacks have lunate tails for fast swimming (cf. Figure 6.6). In side profile, they resemble tuna, but when they turn it can be seen that they are almost flat-sided. These attributes mean they can swim relatively fast, but are sufficiently manoeuvrable to pursue their prey amongst the coral.

Question 7.5

Mass spawning probably has the same advantage as the mass egg laying and hatching of the olive ridley turtles, seen in the introductory programme, i.e. that the predators are overwhelmed by so much food and cannot possibly eat it all (and in this case, the simultaneous spawning is of a number of species, not just one species). Spawning at night would also reduce the chances of a large proportion of the eggs being eaten. In addition, mass spawning of corals of the same species increases the chances of eggs becoming fertilised.

About a week after Full Moon is a time of neap tides (Figure 3.2) and weak tidal currents. This could be an advantage because it means that the eggs and sperm are not spread out or carried away before there is time for fertilisation to occur. (In fact spawning also occurs in calm weather, when wave action is least.)

Question 7.6

- Colours and patterns can be used for display, both for mating (as in the case of the cuttlefish in sequence 11) and for aggression.
- Colours and patterns can be used to aid recognition of animals of the same species, for mating, and to avoid competition.
- They may be used as camouflage, to avoid predation.
- They may be used as camouflage by ambush predators, like the lionfish (which seems to have two 'fake' angelfish in amongst its other camouflage, sequence 7).
- They may also be used to deter or confuse predators – a lot of coral reef fish seem to have large fake 'eyes' on parts of their body other than their heads, while the real eyes are hard to see because of a stripe on the body.

Question 7.7

Corals have adapted to thrive in low-nutrient environments. High concentrations of nutrients favour phytoplankton growth, and nutrient-rich coastal waters are turbid because of large populations of phytoplankton, and this would cut down the light available to the zooxanthellae. More seriously, high nutrient levels would favour benthic algae, and as discussed shortly in connection with El Niño events, these too could harm reefs by smothering them.

Question 8.1

Sealions are eared seals. Perhaps the most obvious clue is that they can turn their hind limbs forward to sit on, and can be remarkably agile on land – which is why they were formerly used in circuses. Their overall shape is that of an eared seal, with a long neck and powerful sloping shoulders.

Question 8.2

(a) The blue whale is the largest animal on Earth and is a baleen whale (Figure 1.8 and Table 8.1), and so it is certainly the largest member of the Mysticeti.

(b) The killer whale – *Orcinus orca* – is a member of the Delphinidae, the dolphins (Table 8.1, Figure 1.8). (Incidentally, porpoises – which are often confused with dolphins – are a separate family altogether: the Phocoenidae.)

Question 8.3

In this sequence, you can see the front flippers being used extensively for swimming and manouevring, rather than lying along the sides (i.e. swimming is *not* by means of moving the hindquarters from side to side). These observations indicate that fur seals are eared seals, but the most conclusive evidence is that ear flaps can actually be seen near the start of the sequence! (In fact, these have to be eared seals because, as mentioned in the text, all fur seals are: eared seals = fur seals plus sealions.)

Question 8.4

(a) The food web shows that although some of the animals (including the largest) are feeding on various planktonic organisms, the rest depend directly or indirectly on the Arctic cod, which therefore plays a pivotal role in the functioning of the marine Arctic ecosystem.

(b) The group of planktonic animals which are conspicuously absent are the gelatinous animals – jellyfish etc. They are not shown because until recently very little was known about them, or their role in food webs (cf. Question 5.6).

Question 9.1

The Atlantic only began to open about 200 million years ago. Eel populations that lived in the bodies of water along the new coastlines may have bred out in the more saline waters and spent the rest of their life-cycle in freshwater. As the Atlantic opened, the distance between their preferred breeding area and the coast gradually increased, but the migratory pattern remained. As you can see from Figure 5.2, the North Atlantic subtropical gyre is asymmetrical, which could explain why the preferred breeding area is now nearer the western coastline than the eastern one. (However, as the Atlantic had been opening for some tens of million of years when the first eels evolved, it seems as if they must always have made quite long migrations, which in itself is rather puzzling.)

Question 9.2

The two words would be *feeding* and *reproducing*. All the migrations described in this Chapter relate to one or other of these activities, and the same is true of migrations on land.

Question 10.1

As shown in Figure 10.1, and mentioned in the caption, the Challenger Deep has a depth of ~ 11 000 m. As hydrostatic pressure increases by about 1 decibar for every metre increase in depth in the ocean, the pressure at 11 000 m depth must be ~ 11 000 decibars.

Question 10.2

'Sea-lilies' (stalked crinoids) are primitive echinoderms, i.e. they belong to the Phylum Echinodermata (see Figure 10.5b, and also Sections 1.1 and 1.2).

Question 10.3

'Dumbo' is a sea-bat. It is drifting over the sea-bed with its tentacles spread so that the membranes between them form a parachute. The 'ears' are, of course, fins (which it flaps up and down). (Also, it is reddish-orange, the usual colour for sea-bats.)

Question 10.4

(a) (1) In surface waters, there is noise produced by rain, waves and turbulence, as well as noise from ships. (2) Surface waters have relatively large populations of all kinds of animals, many of which make sounds, intentionally and unintentionally. With increasing depth below the photic zone, the number of animals decreases dramatically, along with the noise they make.

(b) The sound channel, along which sound travels long distances with relatively little loss in intensity (and which is used by whales for long-distance communication), is generally at about 1000 m depth (Section 4.6).

Question 10.5

Uses of bioluminescence that appear in parts I and II of 'The Deep' (sequences 3 and 5) include:

- Camouflage to avoid predators (like the hatchetfish).
- Camouflage to confuse or startle predators (like the copepod).
- As 'headlights' to help search for prey (like the fish with photophores below its eyes); also for illuminating red prey with red light (the fish with the 'sniper-scope').
- As a lure to attract prey (like the angler fish).
- Attracting a mate (like the female angler fish, and perhaps the firefly squid).
- Communicating in general (like the copepods).

Question 10.6

(a) (i) Animals you may have noted down include: sea-urchins, sea-cucumbers, brittlestars (in the shots of the dark-coloured sea-urchins, but very hard to see), crinoids/sea-lilies, cold-water corals, a tunicate, a polychaete, chimaera, conger eel, six-gilled shark, sleeper shark, hagfish, rat-tails, tripod fish, octopus.

(ii) As mentioned in the narration (and supported by the images), the deep sea-floor is dominated by echinoderms – i.e. the dominant invertebrate phylum on the deep sea-floor is the Echinodermata (which includes sea-cucumbers, sea-urchins and brittlestars, as well as sea-lilies (crinoids) (Figure 1.7)).

(b) The pinkish sea-urchins with the short spines are clearly deposit-feeders, as you can see where they have 'hoovered up edible particles' as they have travelled over the sea-floor. It is likely that the dark-coloured sea-urchins are also deposit-feeders (as are 80% of animals living on abyssal plains); however, it is hard to see how the sea-urchin with the long red-and-white spines feeds on organic material in the sediment!

The sea-lilies and the white coral (*Lophelia*) are clearly suspension-feeders. The mushroom coral is a predator (although it may consume organic detritus as well as zooplankton). The narration suggests that the beautiful swimming sea-cucumber is a deposit-feeder.

Then there are some predators, including the tunicate and the polychaete, and the octopus; the tripod fish is also a predator. Finally, you saw scavengers, feeding on the bodies of dead animals; these included conger eels, six-gilled sharks, sleeper sharks, rat-tails and hagfish. With increasing depth in the ocean, the proportion of predators decreases, and the proportion of scavengers increases. Rat-tails, in particular, play an important role in redistributing food, by scattering the remains of carcases over the deep sea-bed.

Question 10.7

No, because seasonal phytoplankton blooms are a feature of waters in temperate and high latitudes. With the exception of upwelling areas, tropical waters typically have low productivity all year round. Also, as mentioned in Section 4.3, patterns of plankton growth vary from region to region: e.g. in the northern Pacific the amount of organic material sinking to the sea-bed is much less than in the northern Atlantic.

Question 10.8

Cold-water corals do not have any symbiotic algae and so need to obtain *all* their food by capturing it (in the form of organic particles or, in the case of the mushroom coral, zooplankton). In contrast to reef-building corals, they live entirely as suspension-feeders and/or predators.

Question 10.9

(a) Fish with good sight may be able to see other animals by illuminating them using their own luminescent organs (e.g. the fish with the 'sniper-scope' in part II of 'The Deep', sequence 5); also, they may see an animal's own bioluminescence, or bioluminescence accidentally set off in other animals which have been disturbed by water movements (as in the case of the copepods in the same sequence).

(b) Fish make use of sound (Sections 6.5, 8.4.3 and 10.2), and can sense movements in the water using their lateral lines (e.g. the rod-like fish in 'The Deep', part II, sequence 4). They also have a good sense of smell (hagfish, rat-tails and sharks can detect the presence of decomposing flesh from great distances). Sharks and certain other fish (including the chimaera, in 'The Deep', sequence 7) can detect electromagnetic fields (Section 6.5).

Question 11.1

(a) As just discussed, high fish catches are associated with areas of high primary productivity (abundant phytoplankton) (Figures 4.1 and 4.10), which are areas with high concentrations of nutrients, large phytoplankton (particularly diatoms) and relatively short food chains (Figure 5.11b). These areas are along the coasts, and over extensive continental shelves (notably the North Sea and Grand Banks) (Figure 2.4). By contrast, the open oceans are characterised by low nutrient concentrations, small phytoplankton, low primary productivity, long food chains and low biomass of fish and other animals (Figure 5.11a).

(b) The area in question has high primary productivity because of wind-driven upwelling of nutrient-rich waters (Figure 5.3); here, the food chain will resemble Figure 5.11c.

(c) Other areas of the Atlantic which have high primary productivity, and so could support large catches, are the Equatorial Divergence (Figures 4.1 and 4.10), and the Benguela upwelling (Figure 5.4); also, if we are including the Atlantic sector of the Southern Ocean, there is the Antarctic Divergence (Section 5.2.1). In addition to these general areas, there are also the high productivity 'hot spots' associated with seamounts (Section 5.3 and 'Open Ocean', sequence 7).

Question 11.2

As shown in sequence 5 of 'Deep Trouble', destruction that will never show up in 'discard' statistics is that which occurs on the sea-floor, where dredging and deep trawling can damage or kill corals and other invertebrates, and often destroy whole habitats.

Question 11.3

(a) (i) It is very hard to distinguish any patterns or trends in the data, although there seems to have been a general decline in the recruitment of cod, plaice and whiting since the late 1980s. The number of young fish produced each year (and the number surviving to become recruits) is a result of complex interactions between environmental influences and the effects of fishing practices and policies on the spawning stock biomass, so these highly variable data are not surprising.

(ii) For all the species shown, recruitment has on occasion changed by a factor of 3–5 between one year and the next, but the haddock plot shows the greatest variability. There are some marked peaks (particularly in 1967), and in some years recruitment has fallen to a small fraction of what it was the year before.

(b) Herring are a relatively small shoaling species, and feed on plankton – think of the shoals feeding (and being fed on) off Vancouver Island, shown in sequence 11 of 'Seasonal Seas'. Cod are carnivores and grow much bigger – a given region of sea can therefore support many

more herring than cod. (In terms of size, the other species shown fall between the two.)

Question 11.4

(a) No. Off Newfoundland and Labrador, the number of trophic levels fell from seven to six. In the North Sea, the number fell from eight to four. This difference could reflect the fact that the North Sea has been subjected to intensive fishing for even longer than the waters off Canada (Section 11.2).

(b) Generally speaking, in marine ecosystems, the trophic efficiency with which herbivores convert primary production into animal tissue is about 20%, i.e. 0.2 (Section 5.5.2). The second layer up must therefore be about 20% of the volume of the first layer. Trophic efficiencies between higher trophic levels are smaller, closer to 10% (0.1). The very top of the pyramid represents the top predators, many of which are mammals and birds, which, being warm-blooded, convert food to new tissue less efficiently. We would therefore expect the topmost 'layer' to be about 4% of the size of the layer below.

(c) The relevant part of Figure 5.11 is (b), relating to food chains over continental shelves. The food chain in question has *four* levels, compared to seven or eight for the upper pyramids in Figure 11.18. This suggests that the ecosystems on which the continental-shelf food chain in Figure 5.11 (and other published continental-shelf food chains) is based had already been strongly impacted by fishing by the time the data were collected.

(d) Comparison of the volumes of the two pyramids for the North Sea suggests that in 1981 the total annual production of biomass per km^2 of the North Sea was only a quarter or a fifth of what it had been in 1880. (However, as you will see, this is not the whole story.)

Question 11.5

The curves are similar in shape to the curve showing the typical pattern of decline in abundance of large predatory fish, shown in Figure 11.15. By the early 1990s, abundances of these deep-sea fish had fallen by 80%, or even more. These graphs therefore suggest that it may already be too late to protect deep-sea areas where exploitation has already begun, so it is all the more vital to protect those where it has not yet started. (It should be said that these graphs show numbers of fish rather than biomass, as in Figure 11.15, but the message is the same.)

Question 11.6

A positive result of the escapes is that the fish (and their progeny, if any) will swell the population, to some extent taking the pressure off the wild population. This has to be a positive effect. On the negative side, farmed fish may carry a large number of parasites, which could infect wild fish, as well as bacteria or viruses to which wild fish are susceptible. It is also possible that the farmed fish could out-compete wild fish (for perhaps scarce food resources), especially if the former are larger.

A less obvious, more insidious problem arises if the escaped fish breed with wild fish to produce hybrid offspring which are likely to be less well adapted to the environment. For example, salmon are genetically programmed to return to their home river (to which they are adapted) in order to breed. Hybrid offspring may not be able to find their home river: an Atlantic salmon in the Pacific is likely to be rather mystified.

Question 11.7

The problem is that of habitat modification, the alteration or destruction of the coastal environment to allow the aquaculture operation to take place. The most widespread example of this, shown in sequence 11 of 'Deep Trouble', is the destruction of mangroves to allow the construction of prawn and shrimp ponds (particularly ponds for tiger prawns). As you will see, the side-effects of such habitat modification may result in a large decrease in numbers of wild fish.

Question 11.8

- Fish may be dumped at sea if they are caught as by-catch in fisheries where they are not the target species (Section 11.2.2).
- They may also be dumped if the quota for that species has been exceeded (Section 11.2.2).
- Finally, they may also be dumped after they have been landed, if more fish have been caught than can be sold (as with the orange roughy; see sequence 4 of 'Deep Trouble').

Question 11.9

When a fish is mature, it is able to breed, and the older and larger it is, the more eggs it will produce. As discussed in Section 6.1, teleost fish produce thousands or even millions of eggs which are generally released to float in the plankton, where they are an important source of food for small fish ('Open Ocean', sequence 3).

Question 11.10

(1) Dredging and trawling both physically damage organisms on the sea-bed (Section 11.4.3 and 'Deep Trouble', sequence 5); dredging in particular disturbs the sea-bed and animals living on and within it.

(2) Benthic invertebrates living along the coast in the area where the aquaculture operation is set up may be displaced by the enterprise itself (as in the case of prawn farms in mangroves). They may also be affected by effluent from aquaculture operations.

Many benthic invertebrate species have meroplanktonic young (Figure 4.12), and they will be adversely affected by the collection of wild fry to stock aquaculture ponds.

(If your answer was significantly different from this, check whether you have answered the question as asked. For example, in (1) did you discuss overfishing rather than *fishing techniques*? Did you concentrate on the advantageous (rather than adverse) effects on benthic invertebrates, which resulted from the *over*fishing of cod – this was not what the question was about. Did you forget to concentrate on invertebrates (i.e. crustaceans, molluscs, sponges, worms etc.)?)

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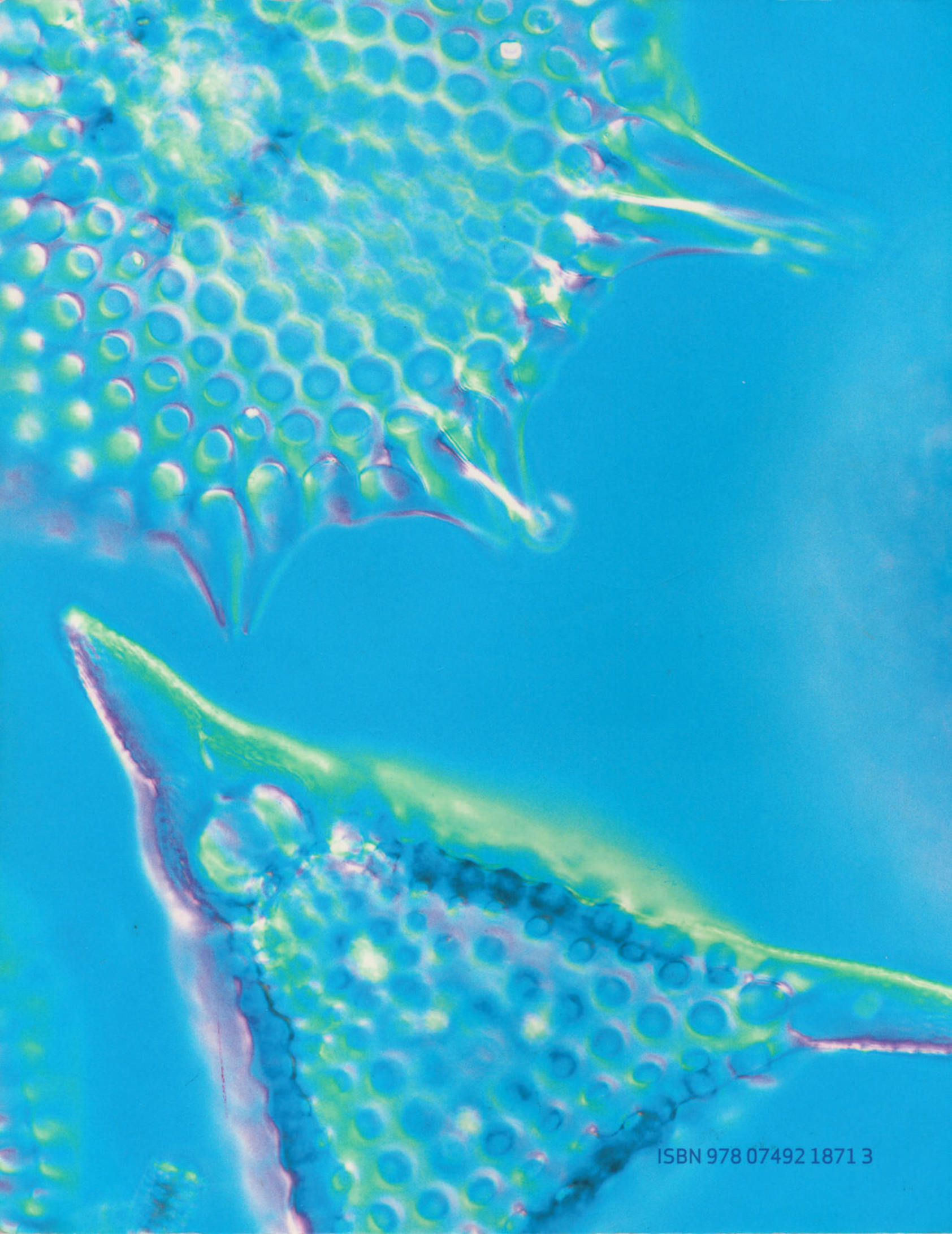

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